

Part 2

INTERSPECIFIC INTERACTIONS

4.1 The nature of interspecific interactions

In Chapters 2 and 3 we examined the consequences of individuals of the same species competing with one another. Natural communities, however, are usually assemblages of species, and in many habitats the 'neighbours' of any one individual may well be of a different species to the individual itself. Yet, although the *process* of interaction between species might occur in a variety of ways (fighting in animals, shading in plants, etc.), there are only three basic *effects*. One species may cause (or be the cause of) increases in the survival, growth or fecundity of another species, or it may cause decreases, or may have no effect at all. Placing these effects in symbolic form in Table 4.1, we can see that there are six possible outcomes, in five of which at least one species is affected.

The most obvious example of the '+ -' type of interaction is a predator-prey relationship in which one species is eaten by the other; but there are other situations in which one species provides a food source or growth requirement for a second species at the first species' expense. Herbivores 'prey' on vegetation but often do not kill entire plants by grazing; and parasites, while reducing the vitality or fecundity of their

host, do not usually cause its immediate death. All aspects of the '+ -' interaction will be considered in detail in Chapter 5.

We can only make passing reference to the '+ 0', '- 0' and '+ +' interactions. This is not to belie their biological significance, but more to indicate the lack of consideration they have received in terms of population analysis. Commensalism (+ 0) is the state in which prerequisite conditions for the existence of one species are maintained or provided by a second, but in which there is no associated adverse effect for the second species. Saprophytism between fungi and higher plants might enter this category, as would 'parasites' that have no measurable effect on their host. The reverse of commensalism is amensalism (- 0), an often-cited example of which is allelopathy between plants: toxic metabolite production by one species causing growth reduction in another. Allelopathy is difficult to investigate in controlled laboratory experiments, and its role in the field is uncertain (see Harper, 1977).

Mutualism (+ +) completes this group of three 'minor' categories, and although it represents a uniquely fascinating topic in evolutionary terms, it has received relatively little attention from population ecologists. Nevertheless, a single example (Janzen, 1966) will illustrate the essential continuity between mutualism and other interactions. The bullhorn acacia of Central America (*Acacia cornigera*) gets its name from the pairs of large, swollen, hollow spines it bears on its trunk. The spines have a patch of thin tissue on one side, and small, aggressive, stinging ants (*Pseudomyrmex ferruginea*) perforate this tissue and nest inside the spine. The ants also feed on nectar produced at the base of the bullhorn acacia leaves, and on protein-rich (Beltian) bodies, produced at the leaf-tips, and they are, therefore, able to complete their whole life cycle on *A. cornigera*. In addition, however, the ants attack any insects that attempt to eat the acacia leaves, and

Table 4.1 The effects of species 1 on survival, growth or fecundity in species 2. The effects of species 2 on survival, growth or fecundity in species 1.

		The effects of species 1 on fitness in species 2		
		Increase	Neutral	Decrease
The effects of species 2 on fitness in species 1	Increase	++		
	Neutral	0+	00	
	Decrease	-+	-0	--

Table 4.2 Effects of the ant *Pseudomyrmex ferruginea* on the bullhorn acacia *Acacia cornigera*. (After Janzen, 1966.)

	Ants present	Ants removed
Weight of suckers (g)	41750	2900
Number of leaves	7785	34600
Average growth in 45 days (cm)	72.6	10.23
Percentage mortality	28	56
Percentage of shoots with other insects		
Day	2.7	38.5
Night	12.9	58.8
Mean number of insects per shoot		
Day	0.039	0.881
Night	0.226	2.707

they cut the shoots of any other plants which come into contact with the acacia and may shade it. As Table 4.2 shows, therefore, the ants, apart from obtaining food and a protected place to live from the acacia, also cause measurable *improvements* in the fecundity and the survivorship of the acacia itself by protecting it from predators and competitors. Fecundity and survivorship are clearly the common currency linking mutualism with every other ecological interaction.

4.2 Interspecific competition

The final interaction in Table 4.1 is interspecific competition, and the '– –' symbolism stresses its essential aspect: that the two species cause *demonstrable* reductions in *each other's* survival, growth or fecundity. Nevertheless, having stressed this, it must also be emphasized that whenever two species compete there will be some circumstances in which one species will be very much more affected than the other. In such 'one-sided' cases of competition it may even be impossible to discern any measurable detrimental effects on the stronger competitor. These cases will *appear* to be amensal. (The relationship between amensalism and interspecific competition is a subtle one which we shall consider in more detail in section 4.11.)

As with intraspecific competition, we can expect that the detrimental effect of interspecific competition

will act through some combination of fecundity and survivorship; that the interaction will be *essentially* reciprocal; that competition will be for a resource which is in limited supply; and that the effects will be density-dependent.

We can, however, expect important differences between the precise nature of interspecific competition in animals and plants. All animals obtain their food from the growth, reproduction and by-products of other living organisms, and they commonly compete for this food. Conversely, the factors required for plant growth, and for which they compete, are neither self-sustaining nor the products of reproductive processes. Moreover, because plants are sessile organisms, they will, once rooted and fixed in position, interfere mainly with their *neighbours'* growth and reproduction (also true of sessile animals, of course). Conversely, amongst most animals there is rarely a continuous struggle between two, or even a few, individuals. Moreover, whereas two plants in close proximity to one another may immediately suggest the possibility of competition for a limited resource (perhaps soil nitrogen, or light in a canopy of leaves), many animal species may never even encounter their competitors (because of differences in foraging strategy, feeding times and so on). In assessing the nature of competitive interactions, therefore, particularly amongst animals, very detailed observation and exacting experimentation are required. Nevertheless, despite these difficulties and differences, there is, as we shall see, a coherent view of interspecific competition which applies to both animals and plants.

4.3 A field example: granivorous ants

Desert environments are of interest to physiologists because of the opportunities they present for studying animals and plants adapted to the extremes of water shortage; but because they are rather simple environments, there are also many instances in which ecological studies in deserts have been very instructive. One example is the work of Davidson (1977a, b, 1978) and Brown and Davidson (1977) on interspecific competition in the seed-eating ants and rodents living in the deserts of the south-western USA. In examining this

example, we shall take the approach which we try to follow throughout this chapter. First, we shall discover whether or not interspecific competition occurs, then we shall examine the form it takes and its consequences.

Seeds play a major role in desert ecology, since they constitute a dormant, resistant stage in the life histories of plants, allowing them to survive the long, unfavourable intervals between short periods of growth. But these seeds are also a food source for several, distantly related taxa (including ants and rodents), which feed as specialized granivores. It is well established that in arid regions mean annual precipitation is a good measure of productivity; and this productivity will determine the size of the seed resource available to these granivorous animals. Thus, the graphs in Fig. 4.1 (Brown & Davidson, 1977) of numbers of common ant and rodent species against mean annual precipitation, indicate that species number is correlated with the size of the seed resource. This suggests that for both granivorous guilds — ants and rodents — the size of the food resource limits the number of common species, and probably also the total number of individuals (a 'guild' is defined as a group of species exploiting the same resource in a similar fashion; Root, 1967). Moreover, by actually

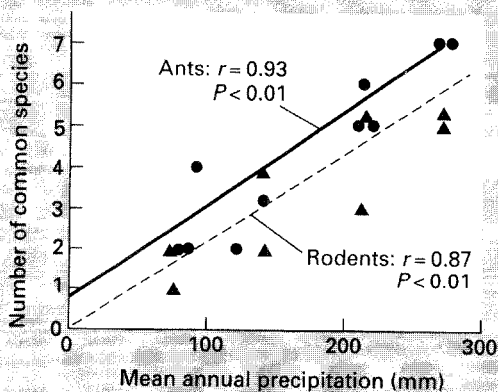


Fig. 4.1 Patterns of species diversity of seed-eating rodents (▲) and ants (●) inhabiting sandy soils in a geographic gradient of precipitation and productivity. (After Brown & Davidson, 1977.)

taking seeds from foraging ants and rodents, Brown and Davidson were also able to show that the two guilds overlapped considerably in the sizes of seeds they ate (Fig. 4.2), suggesting not only that the ants and rodents are limited by their food, but also that the two guilds compete with one another for this limiting resource.

These are only suggestions, however: plausible deductions from field correlations. Realizing this, Brown and Davidson performed an experiment in which four types of 36-m diameter plots were established in relatively level, homogeneous desert scrub. In two plots, rodents were excluded by trapping residents and fencing to preclude immigration; in another two plots, ants were removed by repeated insecticide applications; in two further plots, both rodents and ants were removed and excluded; and, finally, two plots were reserved as unmanipulated controls. The results are shown in Table 4.3, and constitute positive evidence that the two guilds compete interspecifically with one another. When either rodents or ants were removed, there was a statistically

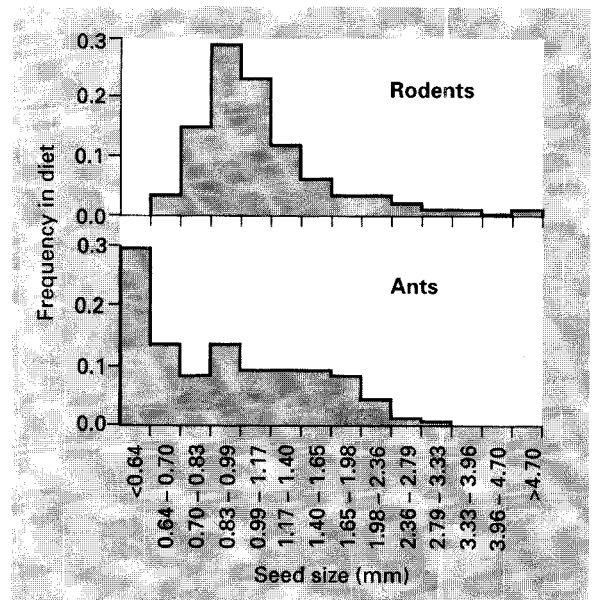


Fig. 4.2 The foods of ants and rodents overlap: sizes of native seeds harvested by coexisting ants and rodents near Portal, Arizona. (After Brown & Davidson, 1977.)

Table 4.3 Competition affects competitors and the resource competed for. Responses of ants, rodents and seed density to ant and rodent removal. (After Brown & Davidson, 1977.)

	Rodents removed	Ants removed	Rodents and ants removed	Control
Ant colonies	543	—	—	318
Rodents numbers	—	144	—	122
Seed density relative to control	1.0	1.0	5.5	1.0

significant increase in the numbers of the other guild; the reciprocally depressive effect of interspecific competition was clearly shown. Moreover, when rodents were removed, the ants ate as many seeds as the rodents and ants had previously eaten between them, as did the rodents when the ants were removed; only when both were removed did the amount of resource increase. In other words, under normal circumstances both guilds eat less and achieve lower levels of abundance than they would do if the other guild was absent. This clearly indicates that the rodents and ants, although they coexist in the same habitat, compete interspecifically with one another. It also suggests strongly that the resource for which they compete is seed.

Davidson (1977a, b) went on from this to examine the various species of ants more closely. She was particularly interested in two facets of the ants' feeding ecology. The first of these was the relationship between a species' worker body length and the size of the seeds which the species harvested. Some of her data are illustrated in Fig. 4.3 (Davidson, 1977a), which represents the results of an experiment in which eight species of granivorous ants were presented with an artificially produced range of seeds and seed fragments of various sizes. Workers and the seeds they were carrying were then sample and measured. The points in Fig. 4.3 refer to mean values, and therefore fail to illustrate the fact that species overlap considerably in the sizes of seed that they take. Nevertheless, it is clear from Fig. 4.3 that seed size and body size are strongly correlated, and that each

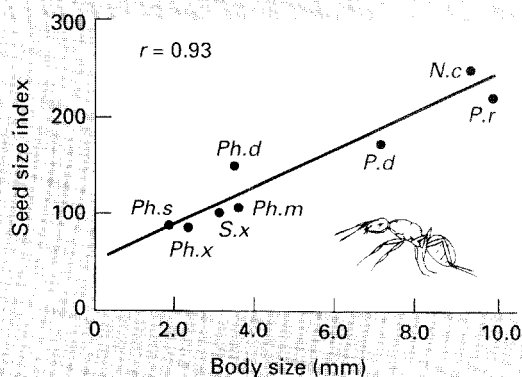


Fig. 4.3 The relationship between worker body length and seed size index for experiments with eight species of seed-eating ants near Rodeo, New Mexico. Species designations are as follows: N.c., *Novomessor cockerelli*; Ph.d., *Pheidole desertorum*; Ph.m., *Pheidole militica*; Ph.s., *Pheidole sitarches*; Ph.x., *Pheidole xerophila*; P.d., *Pogonomyrmex desertorum*; P.r., *Pogonomyrmex rugosus* S.x., *Solenopsis xyloni*. All species except *Pheidole militica* coexist at Rodeo. (After Davidson, 1977a.)

species tends to *specialize* in seeds of a particular size depending on its own size.

The second facet studied by Davidson was the species' foraging strategy (Davidson, 1977b), of which there were essentially two types: 'group' and 'individual'. Workers of group-foraging species tend to move together in well-defined columns, so that, at any one time, most of the searching and feeding take place in a restricted portion of the area surrounding the nest. By contrast, in colonies of individual foragers, workers search for and collect seeds independently of one another, and, as a result, all of the area surrounding the colony is continuously and simultaneously searched. From a series of observations and experiments, Davidson was able to show that group foraging was more efficient than individual foraging when seed densities were high and when the distribution of seeds was clumped; but the relative efficiencies were reversed at low seed densities and when the seeds were more evenly distributed. The situation with regard to foraging is therefore directly comparable with that regarding size. Group and individual foragers show a

considerable potential for overlap in the seeds which they harvest, but each specializes in a particular arrangement of the resource. In fact, the specialization resulting from foraging strategy tends to be a temporal one. Group foragers have marked peaks of activity coinciding with periods of high seed density, and pass less favourable periods in a 'resting' state. Individual foragers, although very active at high seed densities, retain intermediate levels of activity even during the less favourable periods.

Bearing these observations on size and foraging strategy in mind, we can turn now to some of Davidson's (1977a) results concerning the occurrence of various ant species at a range of sites. These are illustrated in Fig. 4.4. It will be convenient, initially, to restrict our discussion to the ant species with mean worker sizes exceeding 3 mm. If we do this, there are several important conclusions we can draw. Almost without exception, when species of similar size coexist

at a site they differ in foraging strategy, and when species of similar foraging strategy coexist at a site they differ in size. The only apparent exception, in fact, is the coexistence of *Pogonomyrmex desertorum* and *P. maricopa* at site A, and of these the latter occurs only rarely. Certainly this should not prevent us from drawing the general conclusion that when several species of granivorous ant coexist at a single site, each specializes in a different way in its utilization of the food resource.

Conversely, when the species compositions of different sites are compared, it is apparent that the species similar in both size and foraging strategy act as 'ecological replacements' for one another. Thus, of the two group foragers exceeding 9 mm in length, *P. barbatus* and *P. rugosus*, only one ever inhabits a site; and of the three individual foragers between 6 and 7.6 mm in length, *P. californicus*, *P. desertorum* and *P. maricopa*, there is never more than one that is

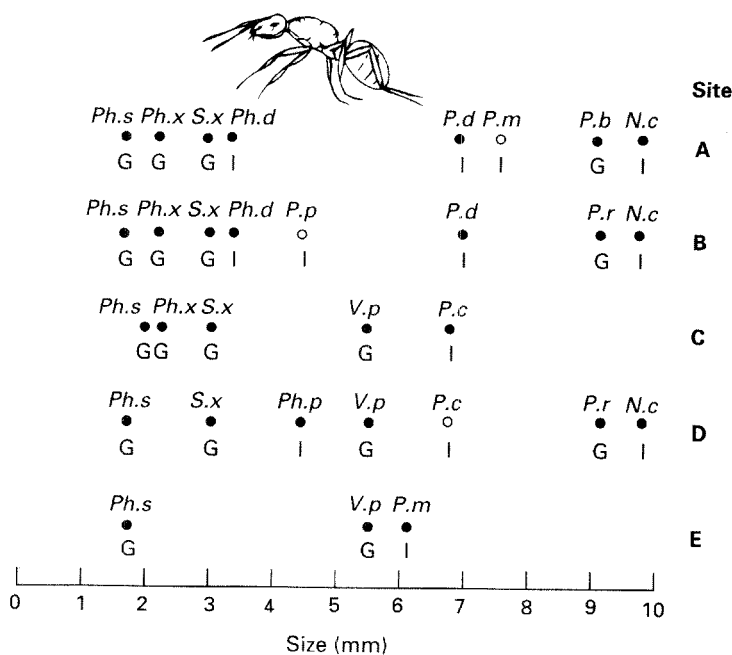


Fig. 4.4 Mean worker body lengths of seed-eating ants at five sites: A, Rodeo 'A', New Mexico; B, Rodeo 'B', New Mexico; C, Casa Grande, Arizona; D, Ajo, Arizona; E, Gila Bend, Arizona. Species designations as for Fig. 4.3 plus *Ph.g.*, *Pheidole gilvescens*; *P.b.*, *Pogonomyrmex barbatus*:

P.c., *Pogonomyrmex californicus*; *P.m.*, *Pogonomyrmex maricopa*; *P.p.*, *Pogonomyrmex pima*; *V.p.*, *Veromessor pergandei*. G, group forager; I, individual forager; species designated by open circles occur only rarely. (After Davidson, 1977a.)

common. Given the numbers of species and sites, this is very unlikely to be mere coincidence. Overall, therefore, it appears that although amongst the guild of granivorous ants there is overlap in resource utilization and interspecific competition for food, there is coexistence only between species that differ in size, or foraging strategy, or both. Species that do not differ in at least one of these respects are apparently unable to coexist.

The data for ant species less than 3 mm in length, however, do not conform to this pattern. It could be claimed that *Pheidole sitarches* and *Ph. gilvessens* are ecological replacement for one another, but, overall, it is apparent that these small species coexist without any differentiation in size or foraging strategy. There are three possible explanations. The first is that the mode of coexistence of the larger species, described above, is not a general phenomenon; these small species compete for a resource and coexist, even

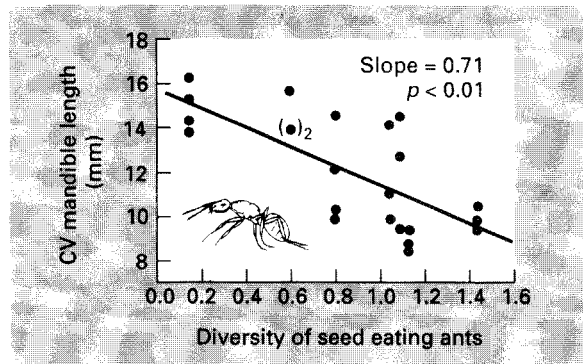


Fig. 4.5 The relationship between the within-colony coefficient of variation (CV) in mandible length for *Veromessor pergandei* and the species diversity of seed-eating ants in the community. (After Davidson, 1978.)

though they utilize the resource in the same way. The second explanation is that the *Pheidole* species do utilize the seed resource in different ways, but at

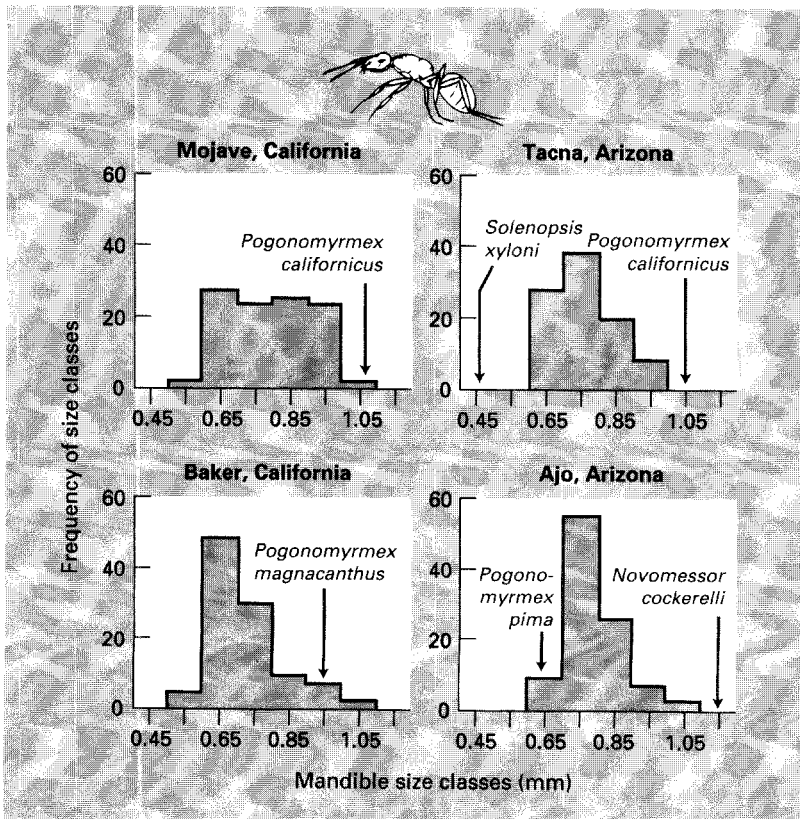


Fig. 4.6 Some frequency distributions of mandible size classes for *Veromessor pergandei*, with the mean mandible lengths of competitors most similar in size indicated by arrows. (After Davidson, 1978.)

present the basis for the differentiation—some third facet of their feeding ecology—is unknown to us. Finally, the third explanation is that these species are not limited and do not compete for the seed resource because they are limited in some other way; perhaps by some other resource, or by a predator that keeps their densities so low that there is no competition.

The most important aspect of these three alternative explanations is that they illustrate some very basic methodological problems in the study of interspecific competition. The second and third explanations are based on our ignorance concerning the ants' ecology; but since we are always likely to be ignorant of a species' ecology to some extent, these explanations can never be discounted. The first explanation is, therefore, left as a last resort: to be used only when we are confident of our own infallibility! Furthermore, these second and third explanations are essentially dependent on there being some 'other' important differences between the *Pheidole* species. Yet the mere discovery of differences between the species cannot, *in itself*, support either of the explanations. The differences must also be shown to reflect differential utilization of a resource for which the species *do* compete. Coexistence requires differences; but there are likely to be many differences that have nothing to do with coexistence. There are, therefore, some very real difficulties in studying interspecific competition (to which we shall return in section 4.1.1). Yet, as we shall see below, concerted effort often confirms that when competing species coexist they do so by differential utilization of the resource for which they are competing.

Finally, Davidson (1978) looked closer still at just one of these species (*Veromessor pergandei*) that differs in size, and size variation, from site to site. Some of her results are illustrated in Figs 4.5 and 4.6. In this case Davidson used mandible length as a measure of size, and, as Fig. 4.5 shows, the variability of this measurement decreased significantly as the diversity of potential competitors at a site increased. In other words, *V. pergandei* is apparently more of a size specialist at those sites in which interspecific competition is most likely, and less of a specialist where it is least likely. This is also apparent from Fig. 4.6, which suggests, in addi-

tion, that size itself is strongly influenced by those species which are most similar to *V. pergandei* in mandible length. The effect is particularly noticeable at Ajo, where *Pogonomyrmex pima* (mean mandible length, 0.64 mm) coexists with *V. pergandei* (0.81 mm). Note that, because of the nature of the data, we cannot conclude with absolute certainty that *V. pergandei* competes with the other ant species for food; but we can say that, at each site, a form of *V. pergandei* has evolved which competes less with the other species than it might have done. Thus, this single, elegant example illustrates four important points.

- 1 Species from distantly related taxa can compete with one another for a limited resource.
- 2 Competition need not lead to exclusion: competitors can still coexist.
- 3 Coexisting species tend to differ in at least one respect in the way they utilize the limited resource, and species which utilize the resource in the same way tend to exclude one another from a site.
- 4 The precise nature of a species, and thus the precise way in which it utilizes the resource, can itself respond to the species' competitive *milieu*.

4.4 Competition between plant species: experimental approaches

Experimental approaches to interspecific competition in plants have followed one or other of two broad pathways. On the one hand, for a particular controlled suite of resources, investigators have altered the number of individual plants present in a two-species mixture, varying either the density or the relative frequency of species, or both. On the other hand, deliberate manipulation of particular resources has been made to assess the responses of competing species. Plants raised from seed or from ramets in a pot are easy to manipulate experimentally and it is not surprising that changes to density in two-species mixtures have provided the main thrust, at least historically.

4.4.1 Manipulating density

Deliberate manipulation of the number of plants in a pot allows the density and proportion of species in

mixture to be changed at will, and, since the plants are together in the same pot, there will, at suitable densities, necessarily be root competition for finite (nutrient and water) resources in the soil, and shading amongst adjacent leaves resulting in competition for incident radiation within the canopy. However, although the execution of a competition experiment may appear straightforward, its design is not. Consider a pot containing a mixture of plants: 100 of species A and 50 of species B. Addition of 50 plants of species B to this pot has two immediate effects. First, it changes the *overall density*, increasing it by a third; but it also alters the *proportion* of species B to A in the mixture from 1/3 to 1/2. In other words, *additive experiments* like this confound two important variables which should, ideally, be clearly separated. One solution to this problem in design is deliberately to maintain the overall plant density constant, but to vary the proportions of the mixture by substitution. The inception and development of the design and analysis of these *substitutive* competition experiments has largely been the work of de Wit and his colleagues in the Netherlands (de Wit, 1960). The basis of the experimental design is the 'replacement series' in which seeds of two species are sown to constant overall density, but the proportions of both species are varied in the mixture from 0 to 100%. At a density of 200 plants we may have 100 A and 100 B, 50 A and 150 B, 0 A and 200 B and so on, representing a set of mixtures all at constant density. Such a series may be repeated at different densities if required.

Figure 4.7 summarizes the types of experimental designs that have been used in investigating competition between two species. In the simplest case of an *additive* design (Fig. 4.7a) species Y is added over a range of densities to a constant density of a target species (X), such that with each addition the overall number of plants per pot increases. Case 4.7b illustrates the *substitutive* design in which the overall density remains constant and the ratio of species X to species Y is varied. In the third design (Fig. 4.7c) all possible combinations of density and frequency are considered such that at any one density there is substitutive series (diagonal combinations, Fig. 4.7c) and there are also addition series for both species

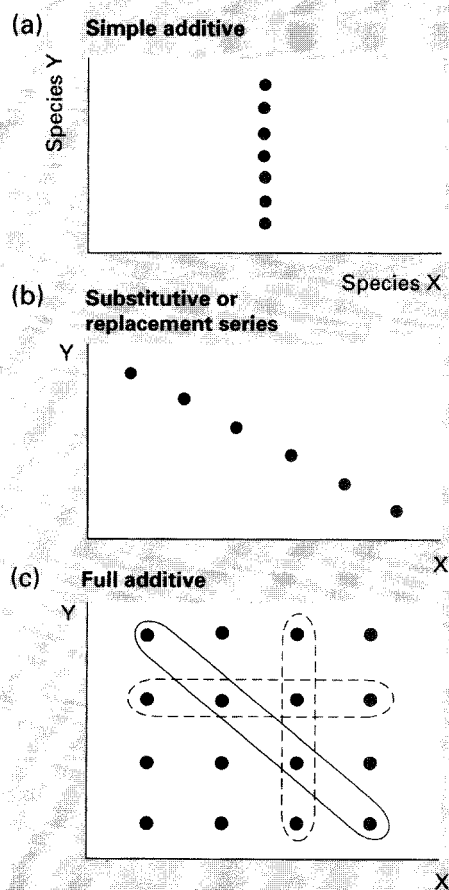


Fig. 4.7 The range of experimental designs used to assess plant competition. ● represents a combination of planting densities of the two species. (See text for details.)

(horizontal and vertical combinations Fig. 4.7c). We will call this a full additive design.

Simple additive experiments have been used by agronomists to demonstrate the outcome of competition between crops (the target species) and weeds and by plant ecologists investigating the effects of neighbours on the yield of a single target plant (Goldberg, 1987). Figure 4.8 illustrates the results of a typical additive experiment, in this case wheat experiencing competition from the weed *Bromus sterilis*. *Bromus* seeds were established over a wide density range (from 0 to over 100 plants) into pots containing a common density of wheat. The design therefore follows

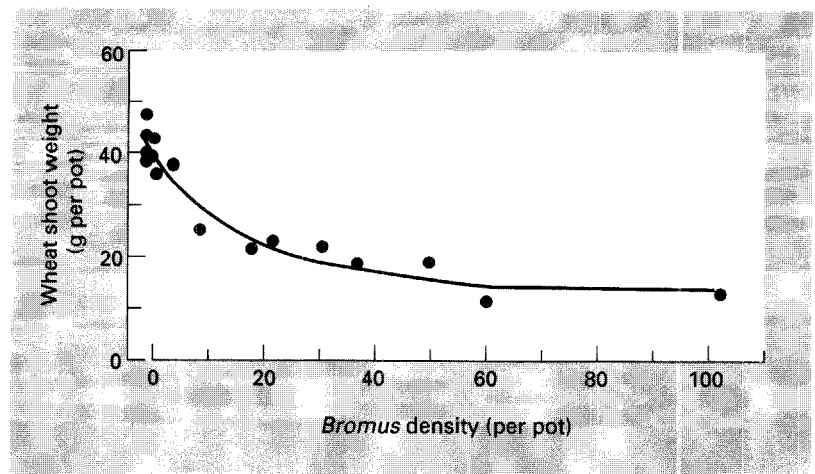


Fig. 4.8 The response of wheat to competition from *Bromus sterilis* in an additive series experiment. (After Firbank *et al.*, 1990.)

Fig. 4.7a in which species X is the wheat and species Y is the *Bromus*. Seeds of both species germinated largely simultaneously, no plants died during the experiment and the yield of the wheat was measured shortly before the plants flowered. We can see (Fig. 4.8) that the yield of the wheat diminishes with increasing density of *Bromus*. Such a yield relationship may be described as hyperbolic, the yield of the target species (wheat) declining towards an asymptote as the density of the added species (*Bromus*) increases.

This form of relationship in simple additive experiments has been widely observed for many plant species (Silvertown & Lovett Doust, 1993). Whilst being useful in practice for empirically ranking the damage done by weed species to a crop it is not possible to disentangle the competitive effect of the weed on crop yield, from the overall effect of increasing total plant density in the mixture. Substitutive designs have therefore been employed to investigate competitive effects at constant total density and an early but exemplary approach of how this may be done comes from work on wild oats.

In the annual grasslands of California two wild oat species, *Avena fatua* and *A. barbata*, occur naturally together, and Marshall and Jain (1969) undertook an experimental analysis of the competitive interaction between them, in order to elucidate the extent and pattern of their cohabitation. The two oats were grown together from seed at four densities—32, 64,

128 and 256 plants per pot—and five frequencies—0, 12.5, 50, 87.5 and 100% of the total sown. After 29 weeks of growth in a greenhouse, the yield of spikelets per pot was assessed for each species. To measure the intensity of intraspecific competition across the range of densities in the mixtures, both species were also grown in monoculture (pure stand). Figure 4.9 shows that the yield per pot in monoculture finally became independent of initial sowing density. This is the background of intraspecific competition against which

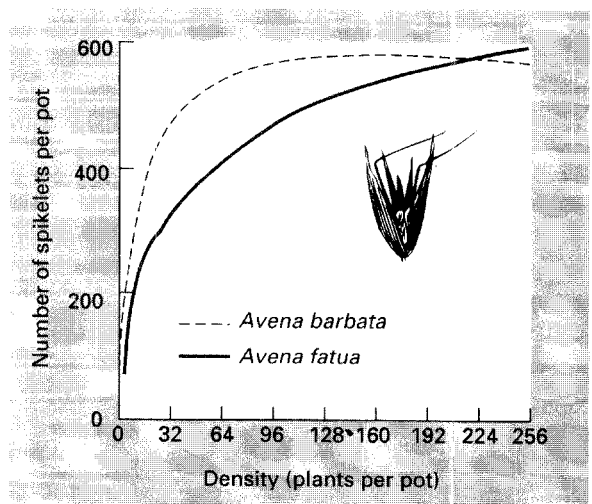


Fig. 4.9 Intraspecific competition in *Avena fatua* and *A. barbata*. (From Marshall & Jain, 1969.)

we must assess the reaction of each species grown in mixture.

Figure 4.10 shows the replacement diagrams for each of the four densities, with yields per pot plotted against the proportion in mixture. The dotted lines in these diagrams are the appropriate yield responses from Fig. 4.9 of each species grown on its own; solid lines show the responses of each in mixture. Comparison of these lines for each species thus allows us to gauge the effect of interspecific competition. At the lowest total density (32 plants per pot), the yield

responses of *A. fatua* in mixture and pure stand are almost identical, suggesting that this species is not responding to the presence of *A. barbata* in mixture. Conversely, for *A. barbata* the yield is depressed so that at the equiproportional mixture it is reduced to only 44%. The interaction appears to be amensal.

Examining the higher planting densities, however, (Fig. 4.10b–d) reveals a truly competitive interaction between the species. The monoculture yield responses are all convex, indicating yield limitation by intraspecific competition. Yet in mixture the yield responses of

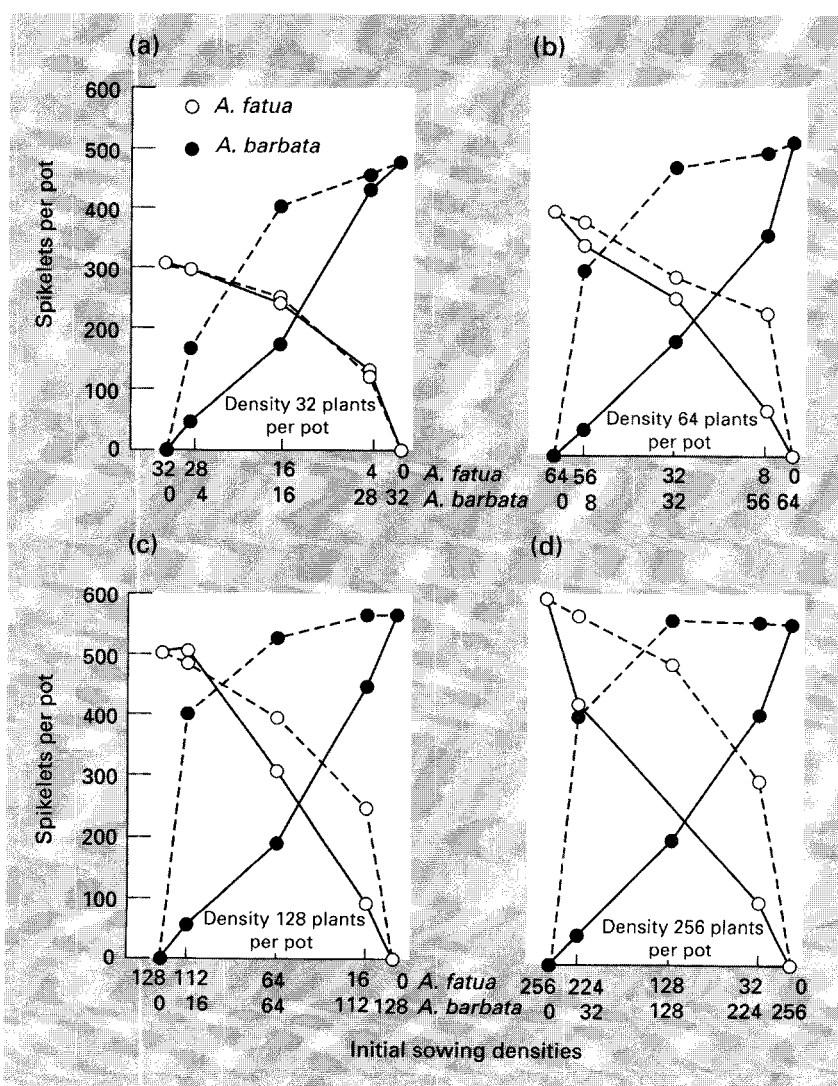


Fig. 4.10 De Wit replacement diagrams for *Avena fatua* and *A. barbata* when grown in mixture at four overall densities. Dotted lines are the yield expectations in monoculture, solid lines the yield in mixture. (After Marshall & Jain, 1969.)

A. barbata are all concave, and with increasing total plant density they become substantially depressed below the expected yield in pure stand. The same is also true for *A. fatua*, since if we examine this species' response in mixture over the four densities, spikelet yield departs more and more from the monoculture expectation. There is, therefore, mutual depression resulting from interspecific competition. However, the shape of *A. fatua*'s response curve changes from convex (Fig. 4.10a), through linear (Fig. 4.10c), to almost concave (Fig. 4.10d). So, whilst suffering interspecific competition, *A. fatua* is performing relatively better than *A. barbata* in mixture: it has a competitive advantage over *A. barbata*; and for both species the intensity of interspecific competition increases with overall density.

Interpretation of replacement diagrams, then, involves two considerations:

- 1 an assessment of what a species might do when growing on its own at densities equivalent to the densities it experiences in the replacement series; and
- 2 a measurement of the departure from this response when grown in mixture.

A response in mixture that is concave necessarily means that a species is suffering interspecific competition, since the yield-density response in monoculture can only be linear or convex (intraspecifically limited). However, a convex response does not mean that a species is not experiencing interspecific competition. We can only assess this with the additional knowledge of the equivalent pure stand response. Our important conclusions from this experiment are (i) that interspecific competition between two plant species may affect the performance of both, but to different extents, i.e. it is asymmetric; and (ii) that the intensity of competition is dependent on the density at which the interaction takes place.

Marshall and Jain's experimental design represents a set of replacement series (four diagonals, see Fig. 4.7b). However, to fully explore the outcome of two-species competition we must use a complete additive design (four diagonals, Fig. 4.7c). Law and Watkinson (1987) grew the sand dune annuals *Phleum arrenarium* and *Vulpia fasciculata* in eight density combinations over a density range of 1–200 plants per

9-cm diameter pot, together with monoculture plantings over the same range. After fruiting was complete, they measured seed yield and examined graphically the response surface arising from competition in relating to the sown density combinations (Fig. 4.11). Comparison of the two surfaces reveals that in general *Phleum* was more sensitive to increases in density than *Vulpia*—yields decline more sharply for *Phleum*, top left to bottom right across the mixtures. More importantly the data suggest that there is an intergrading of the effects of inter- and intraspecific competition across the total plant density range. When present in mixture at low density, both species were sensitive to an increase in the density of the other, a response which diminished with increasing density of the mixture. At the highest sowing density, each species (200 plants per pot), responded little to the presence of the competitor over the entire density range. We may infer from this that the most important competitive interactions at high density tend to be intraspecific ones.

All of the above experimental approaches provide methods that may illustrate the existence of competition between pairs of species but not its long-term outcome over generations, a point we will consider more fully below. Earlier editions of this and other textbooks often refer to a further form of analysis of data collected on a substitutive series design and the use of *relative yields* to suggest whether or not prolonged competition between two plant species will result in competitive exclusion or coexistence. The relative yield of a species in a given mixture is the ratio of its yield in mixture to its yield in monoculture in the replacement series. Calculating yield in this way removes any absolute yield differences that may exist between species and refers both yields to the same scale. The *relative yield total* (RYT) is then the sum of the two relative yields in a mixture. The original proponents of this approach argued that if the RYT of a particular mixture was unity then both species are competing for the same resources for growth in that the relative gain of one species (in numbers and resource acquisition) is exactly balanced by the relative loss of the other. RYT values greater than unity therefore signify differing resource demands—one

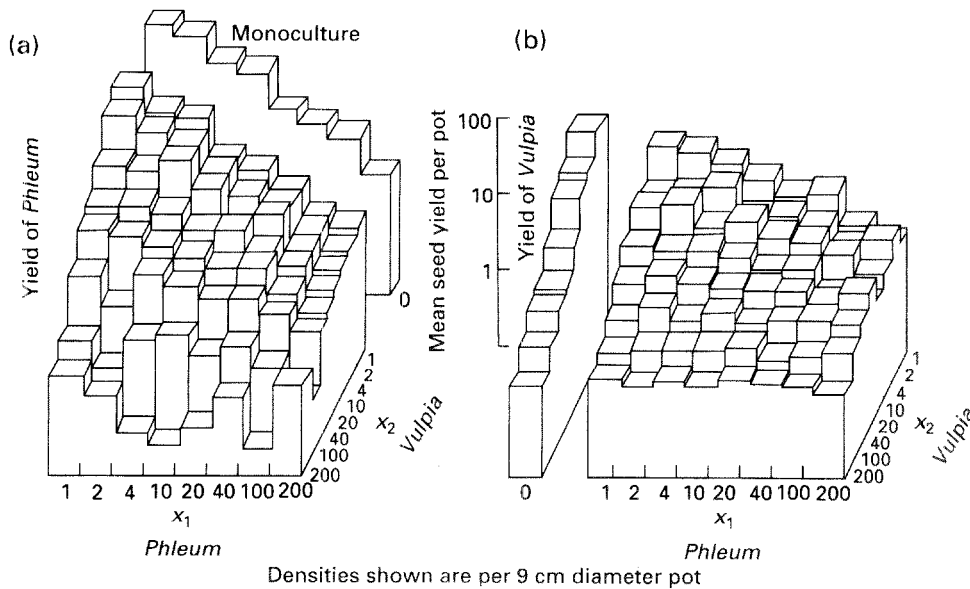


Fig. 4.11 The response surface measured as seed yield per plant of (a) *Phleum arenarium*, and (b) *Vulpia fasciculata* arising from sowing in monoculture and mixture over a range of densities and frequencies. (After Law & Watkinson, 1987.)

species' gain is accompanied by a comparatively minor loss of the other. Figure 4.12 illustrates data analysed in this way. de Wit *et al.* (1966) experimented on a grass legume mixture (*Panicum maximum* and

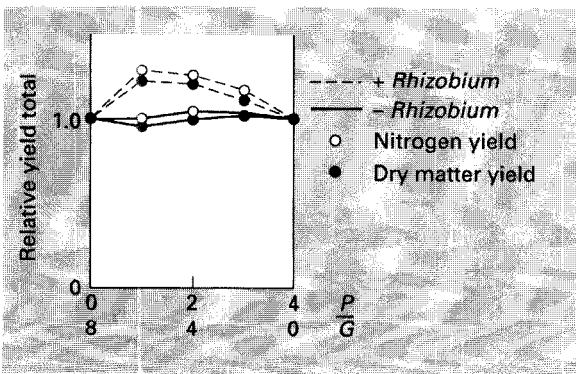


Fig. 4.12 Relative yield totals in the analysis of interspecific competition between *Panicum maximum* (P) and *Glycine javanica* (G) in the presence and absence of *Rhizobium*. (From de Wit *et al.*, 1966.)

Glycine javanica) typical of Australian pastures. The grass *Panicum* can only acquire nitrogen from the soil while *Glycine* acquires part of its nitrogen by nitrogen fixation from the air through its mycorrhizal association with *Rhizobium*. Both species were grown in a substitutive series with and without an inoculation of *Rhizobium*. The RYT's for both dry matter yield and nitrogen content of the plant were not significantly different from 1 in all mixtures in the absence of *Rhizobium*. In contrast, when inoculated with *Rhizobium* in all mixtures investigated RYT's exceeded 1.

The clear inference from this experiment is that when both grass and legume compete for the same nitrogen source (soil nitrogen), the legume will experience such intense competition from the grass that it will ultimately disappear from the mixture; but if the legume is able to utilize a different source, namely nitrogen from the air fixed by *Rhizobium*, then the two species will coexist.

Connolly (1986) has pointed out that the interpretation of RYT's is based on restrictive assumptions. The first is that the yields of the individual species in the monocultures (the 'ends' of the replacement series) are the same as those that would be achieved if each species was grown alone at the constituent densities used over the series. In other words, each species is

sown in mixture and monoculture at a density that gives constant final yield (Chapter 2). Second, RYT's greater than 1 indicate potential coexistence in mixture only at the particular proportion and density investigated. Because of these restrictions, Connolly proposed an index based on a concept of relative resource acquisition by species in mixture. He argued that for a species A grown at a density ($N_{a,x}$) in association with species B (total mixture density, $N_{a,x} + N_{b,x}$) there will be a density N_a in monoculture which will give the same per plant yield (Y) as that observed in mixture. The reciprocal of this density ($1/N_a$), the area occupied by an individual plant, is a measure of the resources needed to achieve Y . The area required to produce the equivalent yield of $N_{a,x}$ individuals with yield Y is then $N_{a,x}/N_a$. By similar argument, the corresponding area for species B is $N_{b,x}/N_b$, where terms are equivalently defined. The *relative resource total* (RRT) is then the sum of these two ratios. If the RRT is greater than 1, the mixture of A and B returns a higher yield than the monocultures and thus this index measures the extent to which species utilize different resources. It should be noted, however, that if RRT is greater than 1, this does not imply that the mixture shows superior yielding to both the monocultures (Connolly, 1986). Further discussion of the strengths and weaknesses of the designs available for investigating plant competition is given by Firbank and Watkinson (1990) and Snaydon (1991).

4.4.2 Manipulating resources

The alternative approach to understanding interspecific competition has developed from the recognition that the methods above describe outcomes of competition but shed little light on the resources which may be limiting and hence on underlying mechanisms. Goldberg (1990) has drawn attention to the distinction between the *effects* of competition and the *responses* to competition. Competing plants will result in a lowering of resource availability but the significance of this reduction depends on the fitness of individuals at the lowered resource level(s) (Fig. 4.13).

The development of our ideas of how competition

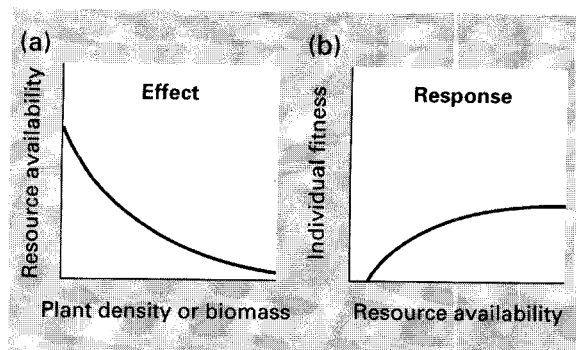


Fig. 4.13 (a) The effect on resource availability caused by plants, and (b) the response to resource availability by plants. (From Goldberg, 1990.)

and coexistence may be determined by resource depletion and species' response to it has come in large part from the work of Tilman (1976, 1982) using planktonic algal species. Silicate and phosphate are essential compounds in the aqueous environment of *Asterionella formosa* and *Cyclotella meneghiniana*, as they are needed for the development of skeletal structure. The growth rate of populations of these single-celled organisms may be expected to be governed by the supply of these compounds in the aqueous environment. From experimental studies, Tilman (1976) showed that the actual growth-rate of each species was determined by the concentration of whichever compound was the more limiting and moreover there were absolute limits below which growth could not occur. He was thus able to quantify the ranges of silicate and phosphate concentration at which both species would exhibit positive population growth-rate, when these compounds were supplied at a constant rate. Figure 4.14a illustrates the fundamental niches of each species with respect to silicate and phosphate. Neither species can inhabit environments characterized as region 1 as the supply of both resources is just too sparse. In region 2, however, silicate levels are above the threshold for net positive growth of *Cyclotella* but not for *Asterionella*. In region 3 the converse is the case, but here it is phosphate that is the limiting resource. In the concentration ranges shown by region 4, populations of both species were not limited by either resource and competition can be

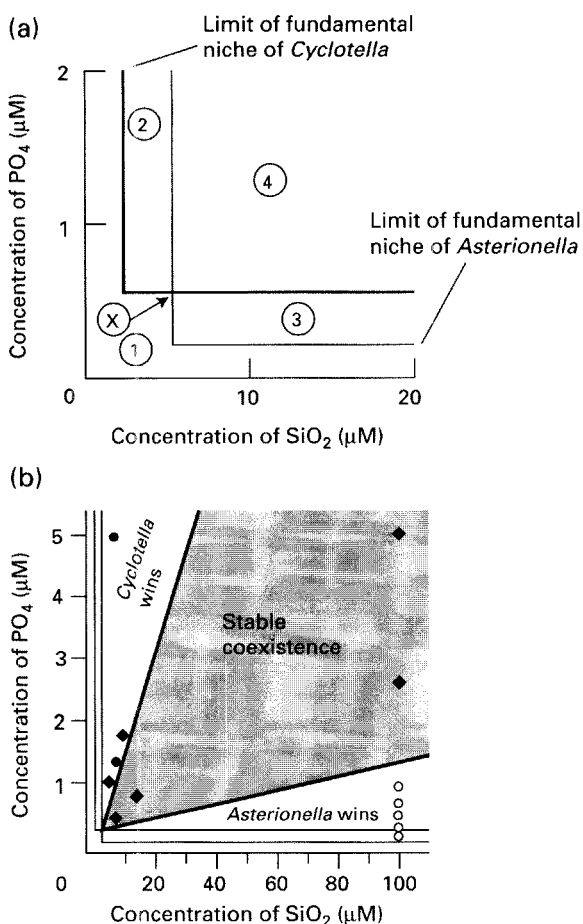


Fig. 4.14 Competition between two algae, *Asterionella formosa* and *Cyclotella meneghiniana*. (a) The fundamental niche of each species is defined. (b) Predicted outcome of competition between the species. Symbols indicate the winners and losers in competition experiments in aqueous environments of varying silicate/phosphate concentration. The predicted outcomes of competition according to the supply of phosphate and silicate are indicated by alternative shading. Data points represent the results of experimental tests of these predictions. In all but two experiments predictions were confirmed. (○), *Asterionella* wins; (●) *Cyclotella* wins; (◆), coexistence of both species. (From Tilman, 1977, 1982.)

expected to occur between them. Tilman postulated that the outcome of competition in region 4 was determined by the relative species' consumption-rates of the two compounds in relation to the supply-rates.

Consider point X (Fig. 4.14a), which is the first combination of resources at which both species may potentially coexist. They will do so only if the ratio of consumption-rate to supply-rate is exactly balanced and sufficient for each species with respect to each resource (i.e. not in region 2 or 4). If consumption of a resource by one species is not matched by supply and the resulting concentration falls below the threshold needed by the other species then competitive exclusion will occur. Thus consumption of phosphate by *Asterionella* in excess of supply rate by the environment will reduce phosphate concentration to a level at which *Cyclotella* cannot persist (region 3, below point X). Similarly, over consumption of silicate by *Cyclotella* will lead to exclusion of *Asterionella*.

Extension of this argument (see Tilman, 1980; Begon *et al.*, 1990) leads to the following conclusion. Competitive exclusion will always occur *unless* each species consumes its more limiting resource at a rate in excess of the supply; or, in other words, coexistence can only arise because of concurrent disproportionate exploitation of the more limiting resource by each species. In Fig. 4.14b, the hatched region illustrates the combinations of silicate and phosphate concentration in which such disproportionate exploitation was predicted to occur, together with experimental tests of these predictions (Tilman, 1982). We can see that pleasingly in all but two circumstances the experiments confirmed the predictions.

In conclusion, these experiments on plants confirm the findings and interpretations of the studies on ants. Two species may compete with one another and coexist, even though the competition has a detrimental effect on both species. Moreover, the conclusion has also been reinforced that for two species to coexist they must in some way avoid making identical demands for limited environmental resources.

4.5 The ecological niche

It is necessary to digress slightly at this point. The term 'ecological niche' has been in the ecological vocabulary for over 70 years, but for more than half of this time its meaning was rather vague (see Vandermeer, 1972 for a historical review). Here, we shall concern

ourselves only with its current, generally accepted meaning, originating with Hutchinson (1957).

If we consider a single environmental parameter (e.g. temperature), then a species will only be able to survive and reproduce within certain temperature limits. This range of temperature is the species' ecological niche in one dimension (Fig. 4.15a). If we also consider the range of humidities in which the species can survive and reproduce, then the niche becomes two-dimensional and can be visualized as an area (Fig. 4.15b); and if a third dimension is added (food particle size in Fig. 4.15c) then the niche becomes a volume. Yet it is clear that there are many biotic and abiotic parameters affecting a species: the number of niche dimensions (n) greatly exceeds three. We cannot visualize such a situation; but we can, by analogy with the three-dimensional model, consider a species' ecological niche to be an ' n -dimensional hypervolume' within which a positive contribution to future generations can be made. And this, in essence, is Hutchinson's conception of the niche. There are, however, several additional, important points which must be understood.

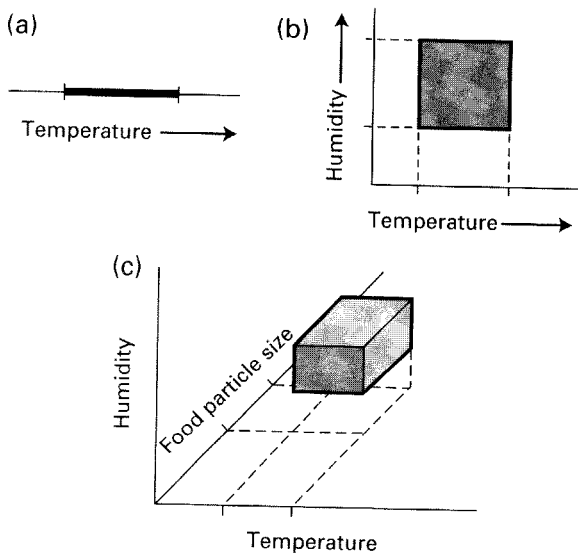


Fig. 4.15 Building up the n -dimensional hypervolume: ecological niches. (a) in one dimension (temperature); (b) in two dimensions (temperature and humidity); (c) in three dimensions (temperature, humidity and food particle size).

1 The ecological niche of a species has been defined from the species' point of view. This allows it to be contrasted with the term 'habitat', which is an objective *description*—in n -dimensions if need be—of the environment itself. Thus, although both niche and habitat are defined in terms of environmental parameters, the term niche characterizes a species, while the term habitat characterizes an environment within which many species may live.

2 Hutchinson gave special consideration to one particular type of environmental parameter: interspecific competitors. The connections between interspecific competition and the ecological niche should become much clearer below, but we can outline Hutchinson's ideas at this stage. He called the niche of a species in the absence of competitors from other species its *fundamental niche*, i.e. the niche which it could *potentially* occupy. In the presence of competitors the species is restricted to a *realized niche*, the precise nature of which is determined by which competing species are present. In other words, Hutchinson wished to stress that interspecific competition reduced contributions to future generations, and that as a result of interspecific competition, contributions in certain parts of a species' fundamental niche might be reduced to zero. These parts of the fundamental niche are absent from the realized niche.

3 A species' niche might also be restricted *in practice* by the habitat: parts of a species' niche—fundamental or realized—which are simply not present at a particular location (in space and time) become, temporarily, irrelevant. This is particularly pertinent to laboratory investigations, in which the simplicity of the habitat confines species to those parts of their niche which happen to be provided by the experimenter.

4 Finally, it must be stressed that the Hutchinsonian niche is not supposed to be a literal description of a species' relationship with its environment. Like other models, it is designed to help us think, in useful terms, about an immensely complex interaction. For instance, the perpendicularity of the volume in Fig. 4.15c is a result of the assumption that the three parameters are independent. Interaction of variables—almost certainly the general rule—would lead to a less regularly shaped niche; but in practice a perpendicular

visualization may be just as useful. Similarly, the solid lines around the niche in Fig. 4.15 ignore the existence of variability within a species. Each individual has a niche, and a species' niche is, in effect, the superimposition of as many niches as there are individuals: a species' niche should have very blurred edges. Once again, however, such sophistication is rarely necessary in practice.

4.6 The Competitive Exclusion Principle

We can now return to our main theme and consider two laboratory investigations of interspecific competition. The first is the work of Park (1954) on the flour beetles *Tribolium confusum* and *T. castaneum*. In a series of simple, sterilized cultures, Park held most environmental variables constant, but varied a single, albeit complex parameter: climate. In all conditions, both species were able to survive in monospecific cultures: the fundamental niches of both species spanned the whole climatic range (Fig. 4.16a). In mixed-species cultures, however, the results were as outlined in Table 4.4. It appears that the climatic extremes are represented in the realized niche of only one of the two species. In the middle of the range there is also, invariably, elimination of one species by the other; but the precise outcome is probable rather than definite. The situation can therefore be visualized as in Fig. 4.16b, with overlapping realized niches in a single dimension.

The second experiment (Crombie, 1947) also concerns two species of flour beetle: *T. confusum* and *Oryzaephilus surinamensis*. Both species can maintain

monospecific populations under a variety of environmental conditions in laboratory cultures of ordinary flour (Fig. 4.16c). In mixed culture of this type, however, *T. confusum* always eliminates *O. surinamensis*; only *T. confusum* has a realized niche (Fig. 4.16d). In such circumstances, *T. confusum* has a higher rate of reproduction and survival, and is also more effective in its destruction of pre-adult individuals. (Both species exhibit this reciprocal predation making it a '– –' and therefore competitive interaction.) However, if an *extra dimension* is added to the environment, namely 'space' (in the form of small glass tubes which are available to *O. surinamensis* but too small to be accessible to *T. confusum*), then *O. surinamensis* gains added protection against predation and there is stable coexistence. Both species now have realized niches (Fig. 4.16e).

The standard interpretation of experiments like these has been elevated to the status of a principle: the so-called 'Competitive Exclusion Principle'. This merely recasts, in terms of niches, what has already been hinted at in granivorous ants and certain plants: if there is no differentiation between the realized niches of two competing species, *or if such differentiation is precluded by the limitations of the habitat*, then one species will eliminate or exclude the other. (As the experiments described above show, such lack of differentiation is often expressed as the total non-existence of the realized niche of one of the species.) Conversely, when differentiation of realized niches is allowed by the habitat, coexistence of competitors is possible.

4.7 Competitive exclusion in the field

Laboratory habitats tend to differ from field habitats in having fewer dimensions, and narrower ranges of those dimensions that they do have. It is likely, therefore, that, in the laboratory, habitat will frequently preclude niche differentiation, forcing potential co-existors to compete in a way that leads to the elimination of one of them. For this reason, field evidence of competitive exclusion is particularly valuable.

Connell (1961) produced such evidence, working in Scotland with two species of barnacle: *Chthamalus stellatus* and *Balanus balanoides*. Adult *Chthamalus*

Table 4.4 Results from the work of Park (1954), see text.

Climate	Percentage wins	
	<i>T. confusum</i>	<i>T. castaneum</i>
Hot-moist	0	100
Temperate-moist	14	86
Cold-moist	71	29
Hot-dry	90	10
Temperate-dry	87	13
Cold-dry	100	0

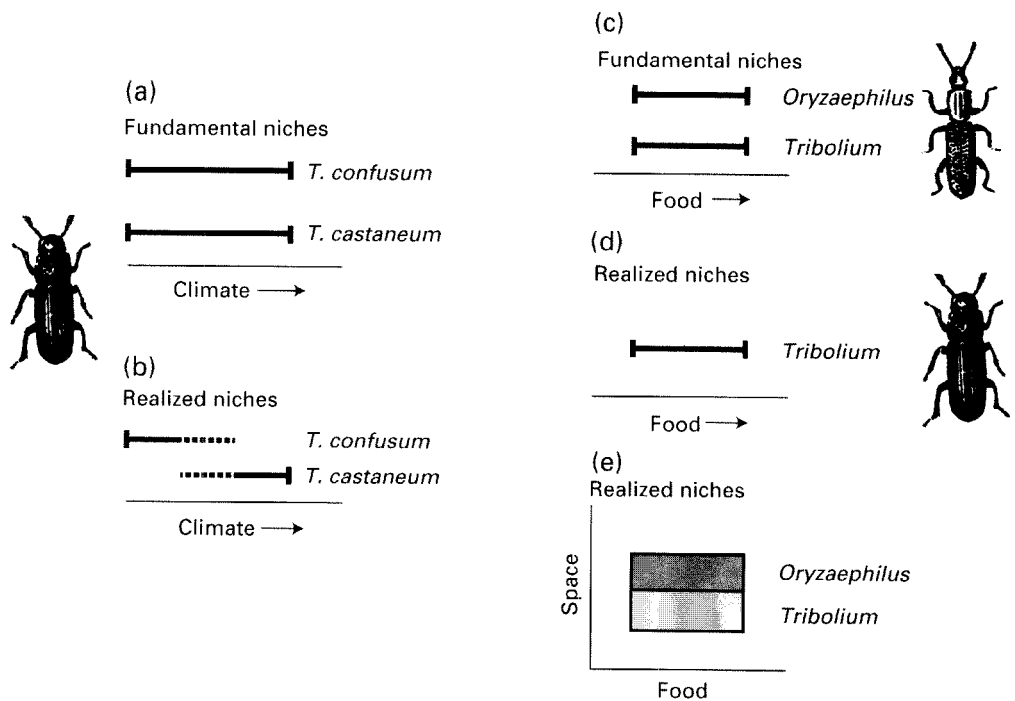


Fig 4.16 (a,b) Indicate, respectively, the fundamental and realized niches of the flour beetles *Tribolium confusum* and *T. castaneum* in relation to climate. (Based on the data of Park, 1954.) (c,d) Indicate, respectively, the fundamental and realized niches of the flour beetles *Oryzaephilus*

surinamensis and *Tribolium confusum* in relation to food, while (e) indicates their realized niches when another niche dimension, space, is added. (Based on the data of Crombie, 1947.) For further discussion, see text.

generally occur in an intertidal zone which is above that of adult *Balanus*. Yet young *Chthamalus* do settle in the *Balanus* zone, so that their subsequent disappearance suggests either that *Balanus* individuals exclude them, or that they are simply unable to live there. Connell sought to distinguish between these alternatives by monitoring the survival of young *Chthamalus* in the *Balanus* zone, taking successive censuses of mapped individuals over the period of 1 year. Most important of all, he ensured at some of his sites that the *Chthamalus* individuals were kept free from contact with *Balanus*. In other words, he carried out a 'removal experiment' allowing him to compare the responses of *Chthamalus* in the presence or ab-

sence of *Balanus*. In contrast with the normal pattern, *Chthamalus* in the absence of *Balanus* survived very well (Fig. 4.17). Thus, it seemed that competition from *Balanus*, rather than increased submergence time, was the usual cause of *Chthamalus* mortality. This was confirmed by direct observation. *Balanus* smothered, undercut or crushed *Chthamalus*, and the greatest *Chthamalus* mortality occurred during the seasons of most rapid *Balanus* growth. Moreover, the few *Chthamalus* individuals that survived a year of *Balanus* crowding were much smaller than uncrowded ones showing, since smaller barnacles produces fewer offspring, that interspecific competition was also reducing fecundity. It is clear, then, that the *fundamental*

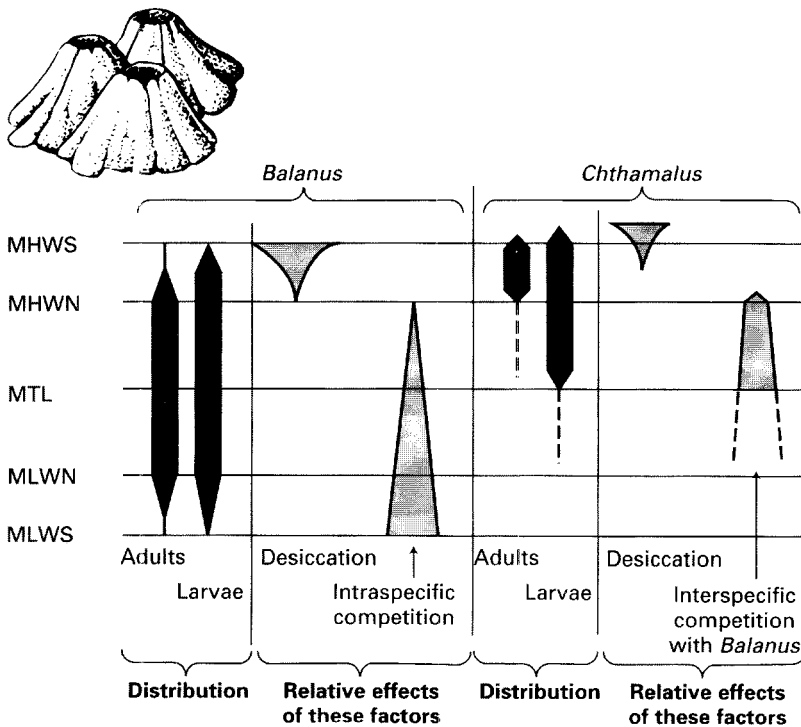


Fig. 4.17 The intertidal distribution of adults and newly settled larvae of *Balanus balanoides* and *Chthamalus stellatus*, with a diagrammatic representation of the relative effects of desiccation and competition. Zones are indicated to the left; from (mean high water-spring) (MHWS) down to (mean low water-spring) (MLWS). (After Connell, 1961.)

niches of both species extend down into the lower levels of the 'barnacle belt'; but interspecific competition from *Balanus* excludes *Chthamalus* from these levels, restricting its realized niche to the upper zones in which it can survive by virtue of its comparatively high resistance to desiccation. It is also clear that competition is markedly 'one-sided' in the lower zones. Yet *Balanus* must expend some of its energy and resources in the process of smothering, undercutting and crushing invading *Chthamalus*, and the two species do undoubtedly compete for the same space. This is, therefore, an example of interspecific competition bearing a superficial resemblance to amensalism.

Another example of competitive exclusion in the field is provided by the work of Inouye (1978) on two species of bumble bee: *Bombus appositus* and *B. flavifrons*. In the Colorado Rocky Mountains, *B. appositus* forages primarily from larkspur, *Delphinium barbeyi* and *B. flavifrons* from monkshood, *Aconitum columbianum*. When Inouye temporarily removed one or other of the bee species, however, the remaining species quickly increased its utilization of its less-

preferred flower. Moreover, it visited more of these flowers than usual during each stay in a patch (such increased stay-times being a recognized indication that the forager is being more successful in the patch). Thus, the fundamental niches of both bee species clearly include both species of flower; and, since it is the presence of one bee species that restricts the realized niche of the other, reciprocal competitive exclusion is strongly suggested. The probable mechanism is as follows: *B. appositus* (longer proboscis) is better adapted to forage from larkspur (long corolla tube) than *B. flavifrons*, but when either bee species is alone the difference is sufficiently slight for both flowers to be valuable sources of nectar. When both bee species are present, however, *B. appositus* depletes the nectar in larkspur flowers to a level which makes them unattractive to *B. flavifrons* (with its shorter proboscis). As a consequence, *B. flavifrons* concentrates on monkshood, depleting the nectar there to a level which makes them significantly less attractive (in cost-benefit terms) to *B. appositus*. The two bee species are, therefore, attracted primarily to different flowers,

and they forage accordingly. This results in reciprocal competitive exclusion.

The *Balanus*–*Chthamalus* interaction and Inouye's *Bombus* study are excellent illustrations of the two contrasting types of interspecific competition (Park, 1954). The aggressive competition by which *Balanus* excludes *Chthamalus* in their joint pursuit of limited space is termed *interference* competition; whereas the reciprocal exclusion of the two *Bombus* species, resulting from the depletion of a resource by one species to a level which makes it essentially valueless to the other species, is termed *exploitation* competition. Thus, with interference there is no consumption of a limited resource, whereas with exploitation there invariably is. (Note that the interference/exploitation dichotomy is somewhat similar to that between scramble and contest (section 2.4), in that contest always involves interference, while scramble usually involves only exploitation. Note, however, that interference and exploitation have none of the extreme threshold or all-or-none characteristics associated with scramble and contest.)

These two field studies are also particularly good examples of competitive exclusion because they are the results of experimental manipulations; the exclusion of *Glycine* by *Panicum* in the absence of *Rhizobium* (section 4.4.1) was equally persuasive. But evidence is much more commonly circumstantial. Remember, for instance, that amongst the larger species of Davidson's granivorous ants there was never coexistence between species that shared both a size and a foraging strategy, i.e. species with apparently very similar realized niches. Providing the number of co-occurrences expected by mere coincidence is much greater than the number observed, reciprocal competitive exclusion is a very *plausible* explanation in such cases; but it can never be more than a plausible explanation when reliance is placed solely on observational data.

4.8 Competitive release

A class of evidence lying between simple observation and experimental manipulation is represented by observations of what is known as 'competitive re-

lease'. Some of the species in the above examples of exclusion show this phenomenon in the special context of an experimental manipulation (expanding their 'range' when a competitor is removed); but the term competitive release is more commonly applied to the results of natural experiments, as in the following example.

The New Guinea archipelago comprises one large, several moderately sized and very many small islands. Species distribution on islands has been extensively studied and analysed (see for instance MacArthur, 1972); but for our present purposes we need note only that in the New Guinea region, as elsewhere, small islands tend to lack species which are present on large islands and on the mainland. One example of this concerns ground doves (Diamond, 1975). As Fig. 4.18 illustrates, there are three similar species of ground dove on New Guinea itself, and moving progressively inland from the coast one encounters them in sequence: *Chalcophaps indica* in the coastal scrub, *C. stephani* in the light or second-growth forest, and *Gallicolumba rufigula* in the rainforest. On the island of Bagabag, however, where *G. rufigula* is absent, *C. stephani* expands its range inland into rainforest; and on Karkar, Tolokiwa, New Britain, and numerous other islands where *C. indica* is also absent, *C. stephani* expands coastwards to occupy the whole habitat gradient. Conversely, on Espiritu Santo *C. indica* is the only species present, and it occupies all three habitats.

This, as Diamond (1975) remarks, is a particularly neat example, but there are many other natural experiments with similar results. Direct interspecific competition has not been positively established, but since *C. stephani* and *C. indica* only occupy rainforest in the absence of *G. rufigula*, *C. stephani* only occupies coastal scrub in the absence of *C. indica*, and *C. indica* only occupies light forest in the absence of *C. stephani*, the conclusion is more or less unavoidable that there is competitive exclusion on New Guinea and competitive release elsewhere.

4.9 Coexistence: resource partitioning

We have seen, from both direct and circumstantial evidence, that competitive exclusion can influence the

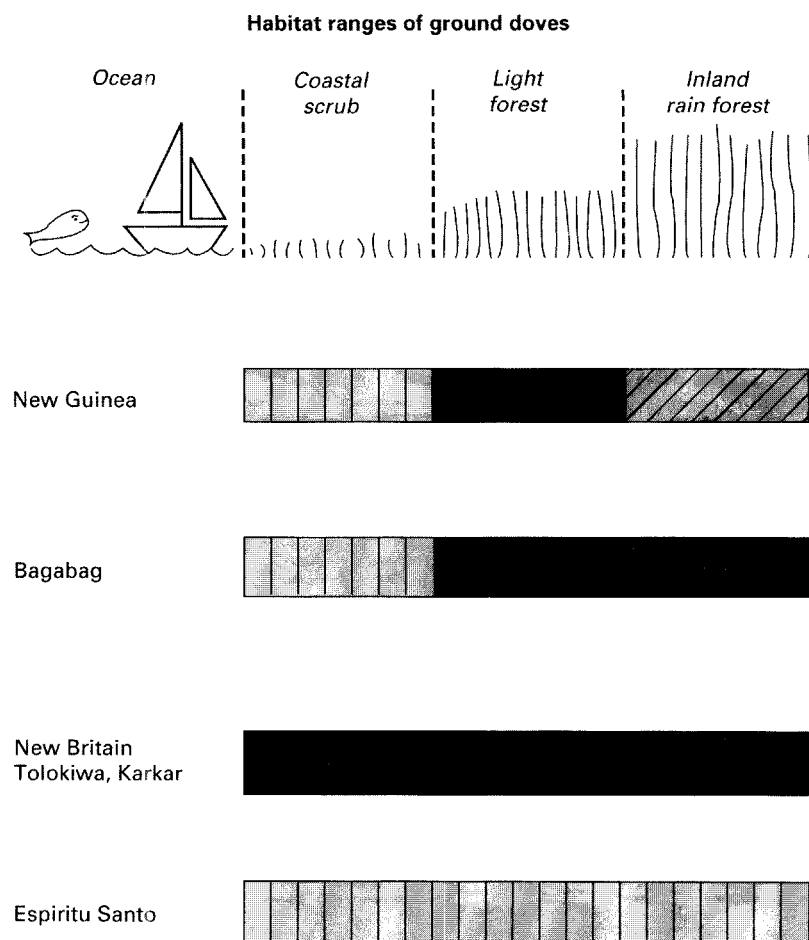


Fig. 4.18 Habitats occupied by three species of ground doves on various islands: *Chalcophaps indica* (vertical bars), *Chalcophaps stephani* (solid shading) and *Gallicolumba rufigula* (diagonal bars). (After Diamond, 1975.)

range and distribution of species. We return now to what is, in a sense, the reverse question: when do similar or competing species coexist?

Vance (1972a) studied competition and the mechanism of coexistence in three sympatric species of intertidal hermit crabs from the San Juan Islands of Washington State: *Pagurus hirsutiusculus*, *P. granosimanus* and *P. beringanus*. The first priority was to confirm that competition was occurring. These hermit crabs are generalized omnivorous feeders and food is apparently abundant throughout the year: *a priori*, the most likely limiting resource was the empty gastropod shells which the crabs inhabit. Vance chose an experimental and a control site, and to the former he added 1000 marked, appropriately sized shells once per month for 1 year. He concentrated on *P. hirsutiusculus*

and estimated densities at both sites at the beginning and end of the year, noting separately (at the experimental site) the numbers in marked and unmarked shells. Despite the fact that many of the empty shells were removed by strong currents, there was a significant increase in total numbers of crabs at the experimental site. However, there was no such increase at the control site, nor in the unmarked shells at the experimental site. Empty shells are obviously a limited resource for *P. hirsutiusculus*. To establish the generality of shell limitation, Vance gathered data on the size distributions of the three species of crabs, of the shells occupied by them, and of unoccupied shells; and he compared these data with the preferred shell sizes of the crabs, determined in preference experiments. Except for small size-classes, empty shells were rare,

and all but small crabs of the three species occupied shells which were smaller than their preferred size. Thus, it appears that empty shells constitute for these three species of hermit crab a common, necessary and limiting resource for which they compete.

Vance went on to examine the mechanism of coexistence of these three species. He found, first of all, that there was partitioning of the resource: *P. hirsutiusculus* prefer short-spined light shells, whereas both *P. beringanus* and *P. granosimanus* prefer relatively taller and heavier shells. He also found that there was partitioning of the habitat: *P. hirsutiusculus* predominates in the upper intertidal and amongst *Hedophyllum sessile*, a brown alga living on horizontal rock faces in the lower intertidal; *Pagurus beringanus* predominates in tide-pools in the lower intertidal; and *P. granosimanus* predominates under large loose stones and in shallow tide-pools of the mid-intertidal. Thus, there is differentiation amongst the realized niches of the three species, allowing them to compete and yet coexist.

The mode of competition between these species appears, essentially, to be interference. Shell occupancy is determined by intra- and interspecific fighting: crabs in less-preferred shells attempting to displace crabs in more-preferred shells, the loser taking the less-preferred shell (Vance, 1972b). We have seen that the outcome of such interspecific encounters is determined to some extent by resource partitioning on the basis of shell shape and weight. However, the basic resource—empty shells—is also divisible into 'shells-amongst-brown-algae', 'shells-in-shallow-tide-pools' and so on; and each species is

apparently specialized in winning fights in a particular area. Thus, what we have called 'habitat partitioning' could also be considered as resource partitioning. Resource partitioning is, therefore, the means by which these three competitors coexist. As Table 4.5 shows, moreover, both types of resource partitioning are necessary for coexistence. *P. beringanus* and *P. granosimanus* are well separated by habitat, but *P. hirsutiusculus* is only truly separated from the other two in shells within its own preference range.

We have obviously met other, similar examples already, though in a slightly different context. *Bombus appositus* and *B. flavifrons* partition the nectar resource on the basis of corolla length: they are adapted to do so by differences in proboscis length. *Balanus balanoides* and *Chthamalus stellatus* partition the space resource on the basis of intertidal zone: *Balanus* is adapted to physically oust its competitor from the lower zones and *Chthamalus* to resist desiccation in the higher zone. *Glycine* and *Panicum* partition the 'total nitrogen' resource: *Glycine* is adapted to utilize free nitrogen by its intimate association with *Rhizobium*. Finally, granivorous ants partition the seed resource on the basis of the size, density and microdistribution of the seeds: they are adapted to do so by differences in their own size and in foraging strategy. In all these cases the basic pattern is the same: competing species appear to coexist as a result of resource partitioning—in other words, by virtue of the differentiation of their realized niches. Moreover, since the same examples have served to illustrate both phenomena, it is clear that resource partitioning and competitive exclusion are

Table 4.5 Hermit crabs occupying *Littorina sitkana* shells (which fall in the *Pagurus hirsutiusculus* preference range) and *Searlesia dira* shells (which fall in the *Pagurus beringanus*–*P. granosimanus* preference range) collected from various physical habitats at a single site. (After Vance, 1972a.)

Habitat	<i>P. hirsutiusculus</i>	<i>P. beringanus</i>	<i>P. granosimanus</i>
Shell species: <i>Littorina sitkana</i>			
<i>Hedophyllum</i> beds	20	0	0
Deep tide-pools, lower intertidal	10	16	2
Cobble bed, mid-intertidal	6	0	32
Shell species: <i>Searlesia dira</i>			
Deep tide-pool, lower intertidal	0	18	1
Shallow tide-pools, mid-intertidal	0	0	26

often, though not always, alternative aspects of the same process. Competitive exclusion between species from portions of their fundamental niches leads to differentiation of their realized niches.

In fact, there are two further patterns which have emerged from the examples we have considered. The species pairs—bees, barnacles and plants—partitioned their resource along a single dimension: corolla length, intertidal zone and total nitrogen, respectively. Conversely, the three species of hermit crab required at least two dimensions: shell shape and weight, and shell location; while the guild of granivorous ants partitioned resources on the basis of seed size and seed density/distribution, and even these two dimensions were apparently not enough to account for the coexistence of the smaller species. There appears, in other words, to be a correlation between the number of species in a guild and the number of niche dimensions involved in the partitioning of the resource. Schoener (1974) reviewed the literature on resource partitioning, and found that this correlation was, indeed, statistically significant. Interestingly, this parallels the results of theoretical investigations by MacArthur (1965) and Levins (1968).

In addition, Schoener (1974), like several others, pointed to the *niche complementarity* frequently involved in resource partitioning. As illustrated by the examples of hermit crabs and, more especially, Davidson's ants, species which are not differentiated along one niche dimension tend to be separated along another. Realized niches are, therefore, fairly evenly distributed in multidimensional space, and species compete simultaneously with several species in several dimensions (called *diffuse competition* by MacArthur, 1972).

Finally, however, it should be clear that we have avoided the most important aspect of competitive exclusion. We have seen that when there is no niche differentiation, competitive exclusion occurs; and we have seen that when competitors coexist there is resource partitioning. But we have ignored a much more profound question. *How much niche differentiation is necessary for the coexistence of competitors?* We return to this question in section 4.15.

4.10 Character displacement

A particular type of resource partitioning, allowing competitors to coexist, is known as character displacement. It involves the modification of the morphological form of a species as a result of the presence of interspecific competitors. Fenchel (1975) investigated the coexistence of hydrobiid mud snails in Limfjord, Denmark, and paid particular attention to two species: *Hydrobia ventrosa* and *H. ulvae*. These deposit feeders seem to ingest their substrate indiscriminately and utilize the attached micro-organisms, and Fenchel found that for both species there is a single linear relationship between shell length and food particle size. Some of Fenchel's results are illustrated in Fig. 4.19. It is clear from this figure that when the two species live alone (which they do in a range of habitats), their sizes are more or less identical, as are the sizes of their food particles. When the two species coexist, however, there is character displacement. *H. ulvae* is larger, *H. ventrosa* is smaller, and the sizes of their food particles are similarly modified. The evidence for interspecific competition is not direct, but there is no simple alternative to the suggestion that the character displacement allows the partitioning of a potentially limiting resource, and thus allows the coexistence of two competitors.

A similar situation, of course, was that described previously for the ant *Veromessor pergandei* (Davidson, 1978), which shows character (size) displacement in response to its competitive milieu: the number and nature of its interspecific competitors. Thus, we can note that, in our newly defined terms, Davidson's ants show competitive exclusion, coexistence through differentiation of realized niches (resource partitioning) and character displacement.

4.11 Competition: its avoidance or its non-existence?

We have seen that species can coexist when, as competitors, they partition resources between them; and also that such partitioning may be achieved, in special cases, by character displacement. But species may also coexist simply because they do not compete.

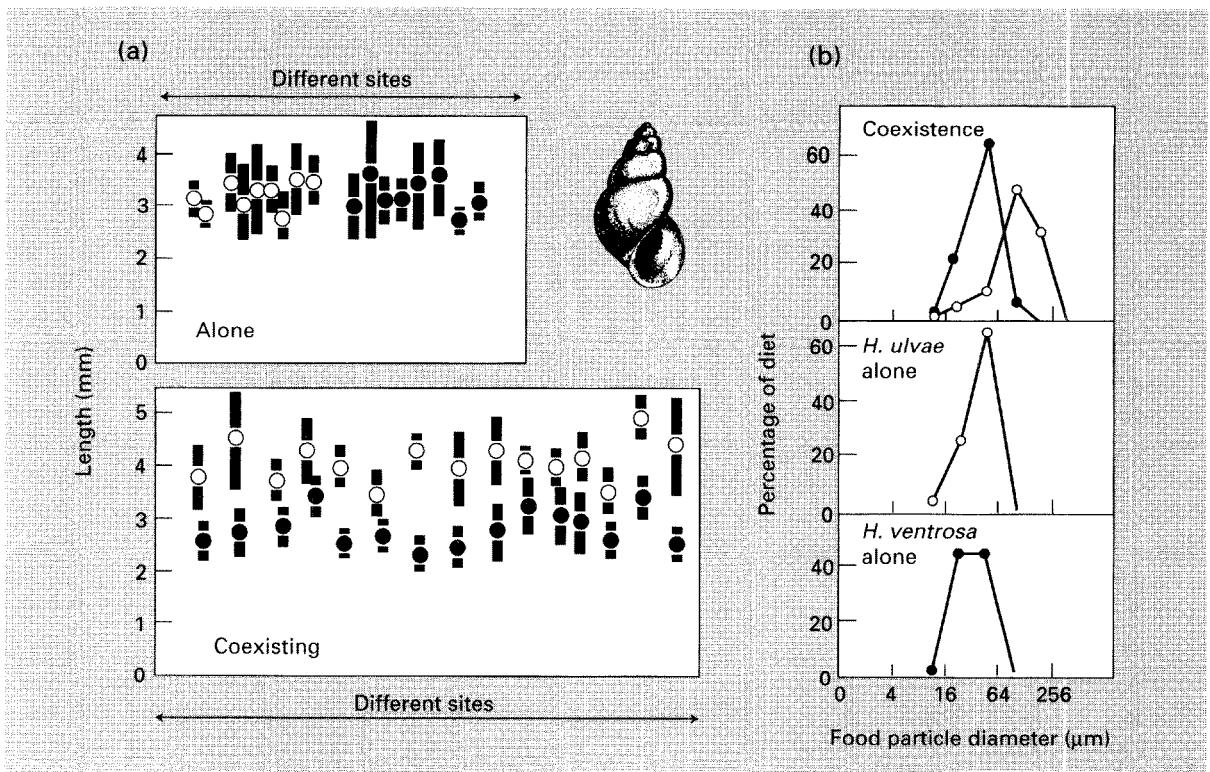


Fig. 4.19 Coexistence through character displacement. (a) Average lengths (plus standard deviations) of *Hydrobia ulvae* (open circles) and *H. ventrosa* (closed circles) at a variety of sites at which they coexist or live alone. (b) Distributions of food particle size of the same species at typical sites at which they coexist or live alone. (After Fenchel, 1975.)

We have tried, until now, to include only those examples in which competition has been positively established. Suppose, however, that Inouye, instead of carrying out his experimental manipulations, had observed simply that two different species of bee forage from two different species of flower, and that the bee species with the longer proboscis foraged from the flower species with the longer corolla tube. The explanation that has been suggested, involving competition, competitive exclusion and resource partitioning, would certainly have been plausible; but there are two alternative explanations. It might have been suggested that each bee species has become so well

adapted to its own flower that there was no (even potentially) shared resource, and therefore no interspecific competition. This explanation implies the existence of interspecific competition in the past, but proposes, in addition, that selection for resource partitioning has been so strong and so longstanding that the partitioning is now complete and irreversible. It might also have been suggested, however, that the difference in proboscis length between *Bombus appositus* and *B. flavifrons* merely reflects the fact that they are two different species, and has nothing to do with competition. There would, therefore, have been a real problem of interpretation if Inouye had relied solely on observational data; and to illustrate this problem we can consider an example of the sort of information that is normally described as 'field evidence of interspecific competition'.

Lack (1971) described the coexistence of five species of tit in English broadleaved woodlands: the blue tit (*Parus caeruleus*), the great tit (*P. major*), the marsh tit

(*P. palustris*), the willow tit (*P. montanus*) and the coal tit (*P. ater*). Four of these congeneric species weigh between 9.3 and 11.4 g on average (great tit 20 g); all have short beaks and hunt for food chiefly on leaves and twigs, but at times on the ground; all eat insects throughout the year, and also seeds in winter; and all nest in holes, normally in trees. Nevertheless, in Marley Wood, Oxford, all five species breed and the blue, great and marsh tits are common.

All five species feed their young on leaf-eating caterpillars, and all except the willow tit feed on beechmast in the winters when it is plentiful; but both of these foods are temporarily so abundant that competition for them is most unlikely. The small blue tit feeds mainly on oak trees throughout the year, concentrating on the smaller twigs and leaves of the canopy to which it is suited by its agility. It also strips bark to feed on the insects underneath, and generally takes insects less than 2 mm in length. It eats hardly any seeds, except those of birch which it takes from the tree itself. The heavy great tit, by contrast, feeds mainly on the ground, especially in winter. Most of the insects it takes exceed 6 mm in length; it eats more acorns, sweet chestnut and wood sorrel seeds than the other species; and it is the only species to take hazel nuts. The marsh tit has a feeding station intermediate between the other two common species: in the shrub layer, in large trees on twigs and branches below 6 m, or in herbage. It is also intermediate in size between the other two species, and generally takes insects between 3 and 4 mm in length. In addition it takes the fruits and seeds of burdock, spindle, honeysuckle, violet and wood sorrel. The coal tit is another small species feeding on oak, but also, later in the winter, on ash. It generally takes insects which are less than 2 mm long, and which are indeed shorter, on average, than those taken by the blue tit. Moreover, unlike the blue tit, the coal tit feeds mainly from branches rather than in the canopy. Finally, the willow tit is most like the marsh tit, feeding on birch and, to a lesser extent, elder, and in herbage. Unlike the marsh tit, however, the willow tit avoids oak and takes very few seeds.

As Lack concluded, the species are separated from each other at most times of the year by their feeding station, the size of their insect prey and the hardness

of the seeds they take; and this separation is associated with differences in overall size, and in the size and shape of the beaks. Yet, as we have seen, there are three possible interpretations of this situation. The first two ('current competition' and 'competition in the past') are based on the assumption that the differences reflect the partitioning by the tits of a potentially limited resource; but the third makes no such assumption. It states simply that the five species, in the course of their evolution, have adapted to their environment in different ways; but in ways that have nothing to do with interspecific competition. And on the basis of the evidence presented, *it is impossible to reject this interpretation*. It has not been shown that the birds would expand their niches in the absence of the other species, and it has not even been shown that food is a limited resource. There is, therefore, no direct evidence of competition, and no overriding reason for involving it in our interpretation.

Nevertheless, the possibility of the first two interpretations does remain. We have seen in several examples—ants, barnacles, bumble bees, etc.—that competing species can coexist by resource partitioning, and can retain the ability to expand their range in the absence of their competitor. Thus, it may be the case that this is also the correct interpretation of the tits' ecology, but that the appropriate experimental manipulations have simply not been carried out.

Moreover, we have also seen—e.g. in the examples of character displacement—that species can evolve morphological adaptations which allow them (largely if not totally) to avoid competition. This (second) interpretation, like the third interpretation (above) denies the existence of current interspecific competition, but unlike the third interpretation it invokes interspecific competition as the evolutionary driving-force behind the differences currently observed.

Indeed, the first and second interpretations are based on alternative outcomes of a shared evolutionary process, which undoubtedly does pertain in some cases. The process occurs as follows. Natural selection favours the survival and reproduction of those individuals with the greatest fitness, but interspecific competition reduces fitness. Individuals that avoid interspecific competition will therefore evolve, and

interspecific competition is avoided by resource partitioning. Evolution of a realized niche which is too small, however, will increase *intraspecific* competition, and this, too, reduces fitness. We can, therefore, expect each species to evolve towards a form in which inter- and intraspecific competition are optimally offset. Sometimes this will evolve relatively flexible resource partitioning (first interpretation); sometimes the partitioning will be inflexible (second interpretation). Sometimes there will be a lessening of interspecific competition; sometimes its total avoidance. Yet in either case, and with either interpretation, interspecific competition will be of paramount importance.

On the available evidence, however, it is impossible to determine whether these tit data indicate interspecific competition (first interpretation), its evolutionary avoidance (second interpretation) or its total non-existence, now *and* in the past (third interpretation); and this would be true of almost all examples of apparent interspecific competition in the field. There are undoubtedly cases of current resource partitioning amongst competitors; and there are undoubtedly cases in which species' ecologies have been moulded by interspecific competition in the past. But differences between species are *not*, in themselves, indications of the ways in which those species coexist; and interspecific competition *cannot* be studied by the mere documentation of these interspecific differences.

Note, finally, that while the first interpretation is based on a ' -- ' interaction, the second interpretation assumes that the interaction is essential '00'. In other words, it is assumed that evolution, acting to avoid 'minuses', converts them to 'zeros'; and this is probably also the basis of most cases of amensalism (- 0). The plant species that produces a toxic metabolite causing growth reduction in a second species presumably does so as an *evolutionary* response to the harmful, competitive effects that the second species had on its growth in the past. At that time the interaction would have been competitive: ' -- ': Now, however, evolution has led to the production of toxin by the aggressive species which occurs *whether or not* potential competitors are present. The aggressive species is, therefore, unaffected by these other species, and the interaction is amensal. Evolution has, in this case,

converted only one of the minuses of a ' -- ' interaction into a zero. In other cases (as in the second interpretation, above) it converts both.

4.12 Competition and coexistence in plants

The theory of the niche and the competitive exclusion principle have their origins firmly rooted in zoological study, and it is intuitively less easy to see how niche differentiation can occur in autotrophic plants, when all have essentially the same basic growth requirements (light, water and nutrients). It might be imagined that plants have evolved specializations to capture energy for photosynthesis from different wavelengths of light, or that nutrients might be utilized in unique and separate ways; but comparative physiological studies show that this is not so. Plant growth requirements ('food') are not usually discrete packages that can be simply partitioned amongst competing species. (An important exception to this however, is nitrogen utilization. The legumes (as we have seen in section 4.4.1), and some other genera such as *Alnus*, do not place total reliance on fixed nitrogen in the soil for growth. Instead, by virtue of their symbiotic relationship with nitrogen-fixing micro-organisms, they utilize free nitrogen from the air.) Moreover, the very nature of the effect of limiting resources on plant growth is complex. Limitation in water supply resulting from intense root competition, for instance, will limit leaf growth; but this may contribute in turn to a reduction in the growth of new roots. Thus, shortage of one limiting resource (water) affects the competitive struggle to obtain both light and water itself. Disentangling the web of cause and effect experimentally has proved very difficult (reviewed by Harper, 1977)

In practice, most attempts to explain the coexistence of plant species have rested largely on a demonstration of the fact that potential competitors differ in ways which might reduce competition. Attention has focused particularly on differences in life form, differences in the timing of various stages of growth—particularly germination and flowering—and differences in preferred levels of abiotic factors (see

Grubb, 1977 and Werner, 1979 for reviews). However, we have seen from the tits in Marley Wood that such differences, taken alone, are impossible to interpret with confidence. The conclusions that can be drawn from such data are severely limited.

Perhaps the most that can be obtained from the interpretation of these differences is illustrated by the work of Werner and Platt (1976). They studied six species of golden rod (*Solidago*) that commonly occur together both in old hayfields undergoing successional change, and in mature, stable prairie communities in North America. In both habitats, but particularly in the prairies, they were able to relate the frequency of occurrence of each species to the availability of soil moisture (Fig. 4.20): different species appear to 'prefer' different moisture levels. There is, of course, no direct evidence that interspecific competition is the driving

force behind this arrangement; but the circumstantial evidence is strengthened in this case by the fact that the degree of separation between species is much greater in the mature prairies than in the young hayfield successional habitats. The position taken up by a species along this environmental gradient is apparently the one at which it has been most successful in competition with the others; interspecific competition, with time, seems to *realize* the niche of each species.

Intuitively, spatial heterogeneity in resource use by plants is probably one of the most powerful promoters of niche separation and coexistence between plants. Species occupying distinct rooting zones within the soil may exploit nutrients and soil moisture sufficiently independently of one another. This can be seen even at the genotypic level. Ennos (1985) observed that genotypes of *Trifolium repens* exhibited different rooting lengths and was able to show that this character was genetically determined. He selected plants having either short or long roots and compared their performance in a replacement series. Under artificially imposed drought conditions the yields of above-ground stolons in 50 : 50 mixtures plantings of the two genotypes significantly exceeded both of the monoculture yields. Bearing in mind the restrictions of this form of analysis, it does seem that the exploitation of different soil layers may enable coexistence in plants.

In a few plant examples, however, it is possible to do more than merely implicate interspecific competition as an important interaction between coexisting species. Sharitz and McCormick (1973), for instance, studied the population dynamics of pairs of annual plant species (*Sedum smallii* and either *Minuartia uniflora* or *M. glabra*) which dominate the vegetation growing on granite outcrops in the south-eastern USA. As Fig. 4.21 shows, there is very strict zonation of the adults of the two species associated with the soil depth around the outcrops; and soil depth itself is strongly correlated with soil moisture. The experimental results in Fig. 4.21b and 4.21c, however, indicate that this zonation is not simply a reflection of the tolerance ranges of the species. In fact, their fundamental niches cover the same range of experimental conditions.

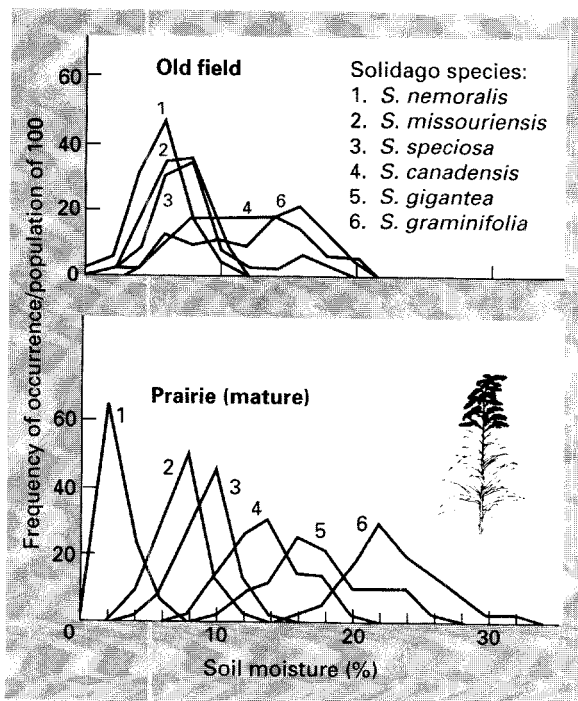


Fig. 4.20 Coexistence of competing plants? The occurrence of six species of *Solidago* in relation to available soil moisture in a hayfield undergoing succession, and in a mature prairie in North America. Soil moisture percentages were determined in summer. (From Werner & Platt, 1976.)

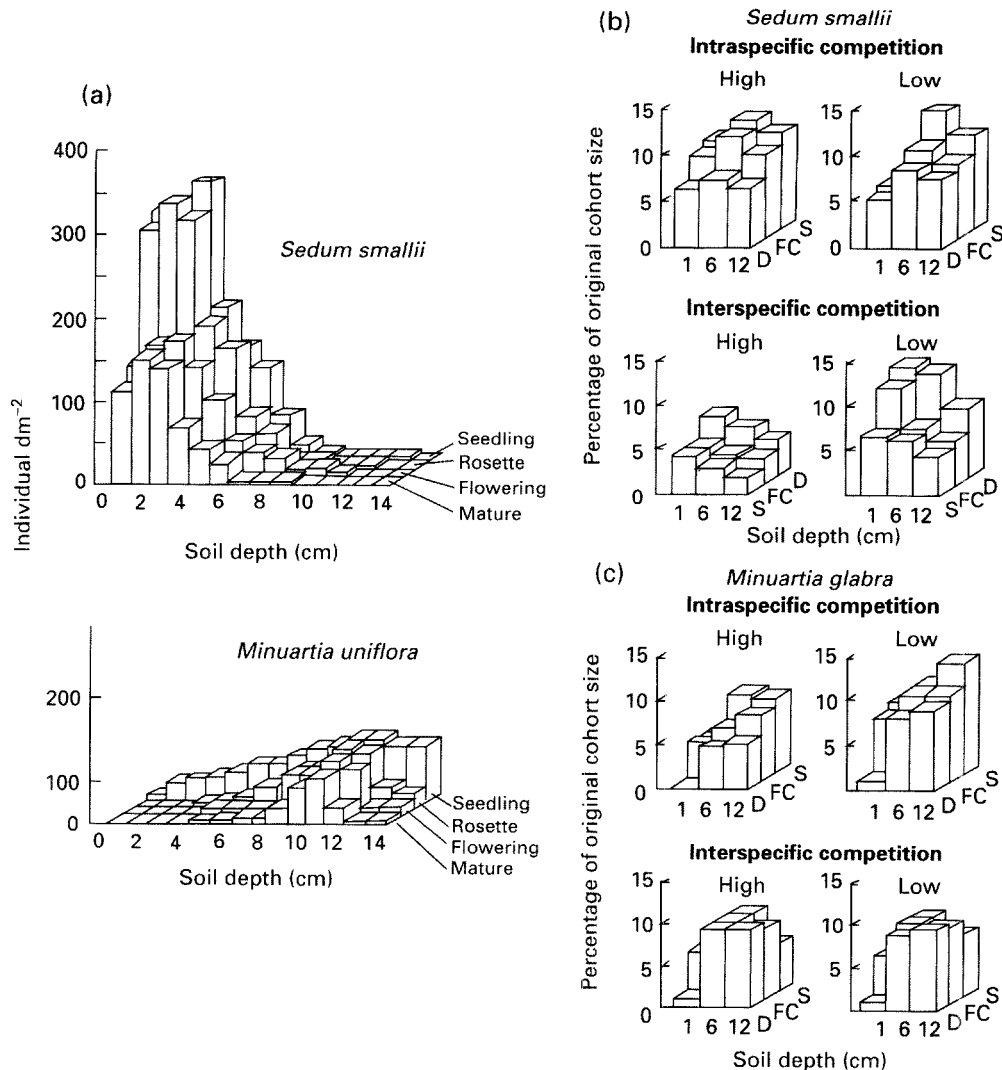


Fig. 4.21 (a) The zonation of individuals, according to soil depth, of two annual plants *Sedum smallii* and *Minuartia uniflora* at four stages of the life cycle. (b,c) The consequences of competitive interaction between *Sedum smallii* and *Minuartia glabra*, respectively. For each species the final density at plant maturity (as a percentage of the

initial seed sown) is shown when grown alone and with the other species. The experiment was conducted at three soil depths and three relative moisture levels: S, saturation; FC, field capacity; D, one-third of field capacity. (From Sharitz & McCormick, 1973.)

Nevertheless, while *Sedum* is clearly more capable than *Minuartia* of tolerating the lack of moisture at the low end of the range, *Minuartia* is obviously much less affected than *Sedum* by interspecific competition at the high end. It is apparent, in other words, that interspecific competition in nature restricts these species to

realized niches (in practice, 'zones') that are significantly smaller than their fundamental niches. Further evidence of this is provided by the very incomplete zonation at the seedling stage, prior to any substantial competitive interaction (Fig. 4.21a). The parallel with the barnacles in section 4.7 is quite striking.

In at least some cases, therefore, plant species which are potential competitors for a limited resource can coexist by virtue of a differentiation of their realized niches. Yet it must be recognized that there are very few instances in which this has been positively established (see Werner, 1979). It is very easy, in plants, to demonstrate the reductions in fitness which can result from interspecific competition; but it has proved very difficult so far to demonstrate the mechanisms which allow potential competitors to coexist. There are two reasons for this. Grubb (1977) has suggested that this difficulty may stem from an overemphasis on adult plants. Irrespective of any niche differentiation, it is almost impossible for a seedling of one species to outcompete an established adult of another species. The most important competition between plants, therefore, may be *pre-emptive* competition for the *regeneration niche*, i.e. competition amongst seedlings to become established in a part of the environment which has recently become vacant. It seems certain that in future, the study of pre-emptive competition will teach us a great deal about the coexistence in nature of competing plants. A very similar phenomenon, restricted to single species and referred to as 'space capture', is discussed in section 6.11.

The second reason is a neglect of the fact that environmental parameters indirectly interact to determine the intensity of competition. Utilization of resources in limited supply may be determined by the species' response to other (non-limiting) environmental factors which govern the competitive outcome. Figure 4.22a portrays the requirements of two hypothetical species for a limiting resource, determined by an abiotic factor such as temperature or pH. At the lower part of the range, species A, by virtue of a lower requirement for the limiting resource will tend to outcompete species B. The converse will be true in the upper part of the range. In mid-range, all other factors being equal, growth is limited to the same extent and coexistence occurs. Partial support for this view comes from a further experiment using the planktonic algal species *Asterionella formosa* and *Synedra ulna* (Fig. 4.22b). Over much of the temperature range (4–20°C), *Asterionella formosa* has the lower requirement for

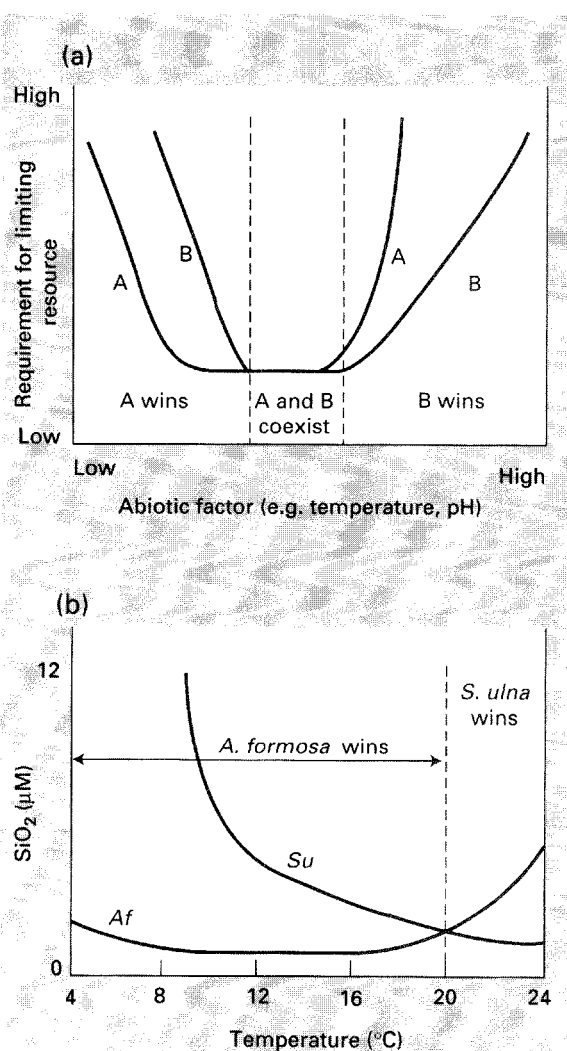


Fig. 4.22 (a) Competition for one limiting resource in relation to an abiotic factor. (b) The outcome of competition for silicate for two species of planktonic algae over a wide temperature range. *A.f.*, *Asterionella formosa*; *S.u.*, *Synedra ulna*. (Modified from Tilman et al., 1982.)

SiO_2 and outcompetes *Synedra ulna*, but the reverse is true above 20°C. Although there is no temperature range in which both species have the same demand for silicate, we can envisage coexistence if there are fluctuations in temperature over the range in which alternative competitive displacement can occur. Indeed, diurnal temperature fluctuations between 16

and 24°C are very likely in the surface waters of the lakes in which these species live. The only proviso that we must add in final explanation of this mechanism is that it clearly depends on the time scale over which population growth responses can occur.

4.13 A logistic model of two-species competition

Having examined what is known about interspecific competition, it will be valuable to turn (as we did with single-species populations) to some simple models, to see whether they can improve our understanding of the interaction.

The conventional starting point for such models is the differential *logistic equation* (following Lotka, 1925; Volterra, 1926). Obviously, therefore, in conforming to this convention, we will be incorporating into our model all of the logistic's shortcomings. Nevertheless, as will become apparent below, a useful model can be constructed.

The logistic equation:

$$\frac{dN}{dt} = rN \left(\frac{K - N}{K} \right)$$

contains, within the brackets, a term which is responsible for the incorporation of intraspecific competition. We can proceed by replacing this term with one which incorporates not only intra- but also interspecific competition. We will denote the numbers of our original species by N_1 (carrying-capacity, K_1 ; intrinsic rate of increase, r_1), and those of a second species by N_2 .

Suppose that, together, 10 individuals of species 2 have the same competitive, inhibitory effect on species 1 as does a single species 1 individual. The *total* competitive effect on species 1 (inter- and intraspecific) will then be equivalent to $(N_1 + \{N_2/10\})$ species 1 individuals. We call the constant—1/10 in the present case—a *coefficient of competition*, and denote it by α_{12} since it measures the competitive effect *on* species 1 *of* species 2. In other words, multiplying N_2 by α_{12} converts it to a number of ' N_1 -equivalents'. (Note that $\alpha_{12} < 1$ means that species 2 has less inhibitory effect on species 1 than species 1 has on itself, while $\alpha_{12} > 1$ means that species 2 has a greater inhibitory effect

than species 1 has on itself.) We now simply need to replace N_1 in the bracket of our logistic equation with a term which signifies: ' N_1 plus N_1 -equivalents', i.e.

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - [N_1 + \alpha_{12} N_2]}{K_1} \right)$$

or

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha_{12} N_2}{K_1} \right).$$

We can, of course, write a similar equation for species 2:

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - \alpha_{21} N_1}{K_2} \right).$$

This is our basic (Lotka–Volterra) model.

To describe the properties of this model, we must ask the following questions: when (under what circumstances) does species 1 increase in numbers? When does it decrease? And, when does species 2 increase and decrease? In order to answer these questions we construct what are, in essence, the equivalents of maps. Thus, while in maps there are areas of land and areas of sea, with a coastline (neither land nor sea) dividing them; in our case we will have areas of N_1 (or N_2) increase and areas of N_1 (or N_2) decrease, with a *zero isocline* (neither increase nor decrease) dividing them. Moreover, if we begin by drawing a zero isocline (coastline), we will know that there is increase (land) on one side of it and decrease (sea) on the other. As Fig. 4.25 shows, the axes of our 'map' will be N_1 and N_2 : the bottom left-hand corners are areas where there are low numbers of species 1 and 2, and the top right-hand corners areas where there are high numbers of species 1 and 2.

In order to draw the N_1 -isocline we will use the fact that on it $dN_1/dt = 0$, i.e.

$$r_1 N_1 \left(\frac{K_1 - N_1 - \alpha_{12} N_2}{K_1} \right) = 0.$$

This is true for two trivial cases (when r_1 or N_1 are zero), but also for an important case:

$$K_1 - N_1 - \alpha_{12} N_2 = 0$$

or

$$N_1 = K_1 - \alpha_{12}N_2.$$

Indeed, the straight line represented by this equation is our isocline, and since it is a straight line we can draw it by finding two points on it and joining them. Thus when

$$N_1 = 0, N_2 = \frac{K_1}{\alpha_{12}} \quad (\text{point A, Fig. 4.23a})$$

and when

$$N_2 = 0, N_1 = K_1 \quad (\text{point B, Fig. 4.23a}).$$

The line in Fig. 4.23a is, therefore, the N_1 -isocline. Below and to the left of it, numbers are low, competition is comparatively weak and species 1 increases in abundance (arrows from left to right, N_1 on the horizontal axis); above and to the right of it, numbers are high, competition is comparatively strong and species 1 decreases in abundance (arrows from right to left).

Based on an equivalent derivation, Fig. 4.23b has areas of species 2 increase and decrease separated by the (straight) N_2 -isocline; arrows, like the N_2 -axis, are vertical.

All that is required now is to put the N_1 - and

N_2 -isoclines together on a single figure. In so doing, it should be noted that the arrows in Fig. 4.23 are actually vectors—with a strength as well as a direction—and that, to determine the behaviour of a joint N_1 - N_2 population, the normal rules of vector addition should be applied (see Fig. 4.24). It is clear from Fig. 4.25 that there are four different ways in which the two isoclines can be arranged. In Fig. 4.25a and 4.25b, one isocline lies entirely beyond the other, and the vectors indicate that, as a consequence, the species with the inner isocline becomes extinct, while the other species attains its own carrying-capacity.

Such situations can be defined by the intercepts of the isoclines. In Fig. 4.25a, for instance:

$$\frac{K_1}{\alpha_{12}} > K_2 \text{ and } K_1 > \frac{K_2}{\alpha_{21}}$$

i.e.

$$K_1 > K_2\alpha_{12} \text{ and } K_2 < K_1\alpha_{21}.$$

Species 1 exerts more effect on itself than species 2 exerts on it, but also exerts more effect on species 2 than species 2 does on itself. In other words, species 1 is a strong interspecific competitor, species 2 is a weak interspecific competitor, and species 1 drives species 2 to extinction. The situation is reversed in Fig. 4.25b.

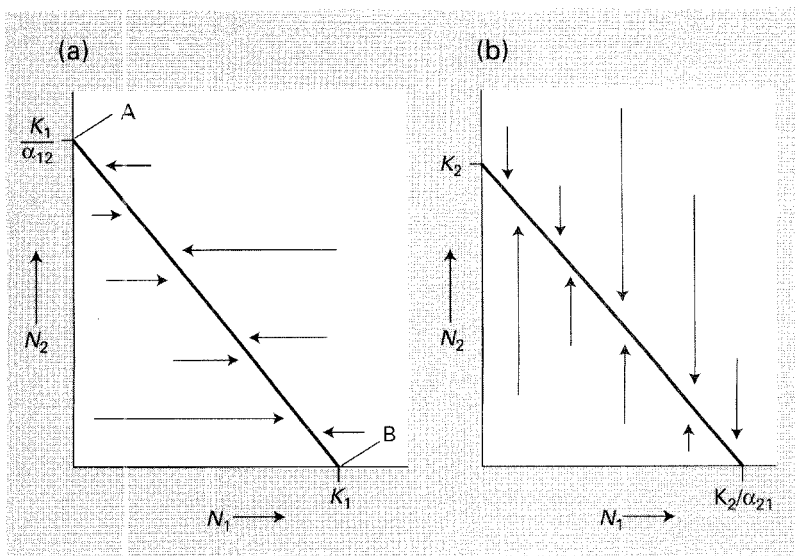


Fig. 4.23 (a) The N_1 -isocline generated by the Lotka–Volterra competition equations. Species 1 increases below and to the left of the isocline (arrows left to right), and decreases above and to the right of the isocline (arrows right to left). (b) The equivalent N_2 -isocline.

In Fig. 4.25c:

$$K_2 > \frac{K_1}{\alpha_{12}} \text{ and } K_1 > \frac{K_2}{\alpha_{21}}$$

i.e.

$$K_1 < K_2 \alpha_{12} \text{ and } K_2 < K_1 \alpha_{21}.$$

Interspecific effects are more important than intraspecific effects: both species are strong interspecific competitors. There are two stable points ($N_1 = K_1, N_2 = 0$ and $N_2 = K_2, N_1 = 0$) and an unstable equilibrium combination of N_1 and N_2 . In other words, one species always drives the other to extinction, but the precise outcome depends on the initial densities.

Finally, in Fig. 4.25d:

$$\frac{K_1}{\alpha_{12}} > K_2 \text{ and } \frac{K_2}{\alpha_{21}} > K_1$$

i.e.

$$K_1 > K_2 \alpha_{21} \text{ and } K_2 > K_1 \alpha_{21}.$$

Intraspecific effects are now more important than interspecific effects, both species are weak interspecific competitors, and there is stable coexistence at a particular, equilibrium combination of N_1 and N_2 .

4.13.1 The model's utility

We can now proceed to examine this simple model's utility. Clearly, it can produce the full range of outcomes of interspecific competition: stable coexistence, predictable exclusion of one species by another, and exclusion between the two species with an indeterminate outcome. It should be recognized, however, that these are the only conceivable outcomes; to be useful, the model must produce the right outcome at the right time.

The model indicates (Figs 4.25a & 4.25b) that one species will outcompete and exclude a second if the first species is a stronger competitor on the second than the second is on itself, and the effect is not reciprocated. We saw in section 4.7 that this was, indeed, the case for each bumble bee on its own flower (exploitation competition), and for *Balanus* excluding *Chthamalus* (interference competition). In other words,

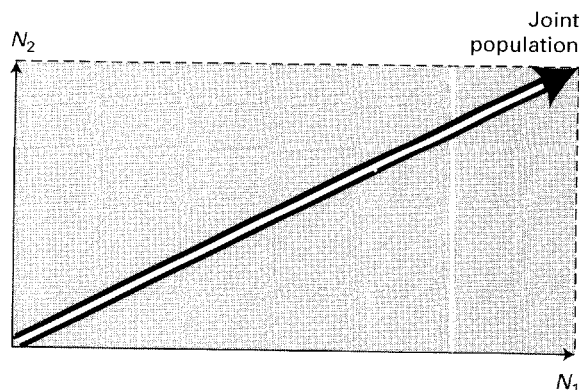


Fig. 4.24 Vector addition. When species 1 and 2 increase in the manner indicated by the N_1 and N_2 arrows (vectors), the joint population increase is given by the vector along the diagonal of the rectangle, generated as shown by the N_1 and N_2 -vectors.

Fig. 4.25a and 4.25b successfully describes situations in which the second species lacks a realized niche in competition with the first.

In Fig. 4.25c, both species are stronger competitors on the other species than they are on themselves: there is reciprocal interference competition. This will occur when each species produces a substance that is toxic to the other species but harmless to itself, or when there is reciprocal predation. In fact, this latter situation is the mechanism by which Park's flour beetles compete (section 4.6), and it is satisfying, therefore, to see that the model's predictions are borne out by Park's data: there is competitive exclusion, but the precise outcome is indeterminate. Whichever species starts with (or, at some point, attains) a more favourable density will 'outpredate' (or outpoison) the other.

Finally, Fig. 4.25d indicates, quite reasonably, that stable coexistence is only possible when, for both species, intraspecific competition is more inhibitory than interspecific competition, i.e. when there is niche differentiation. We have seen repeatedly that this is the case. However, the model avoids the more profound question of *how much* niche differentiation is necessary for stable coexistence.

It is clear, then, that in broad terms the model is successful in spite of its limitations. Indeed, it is

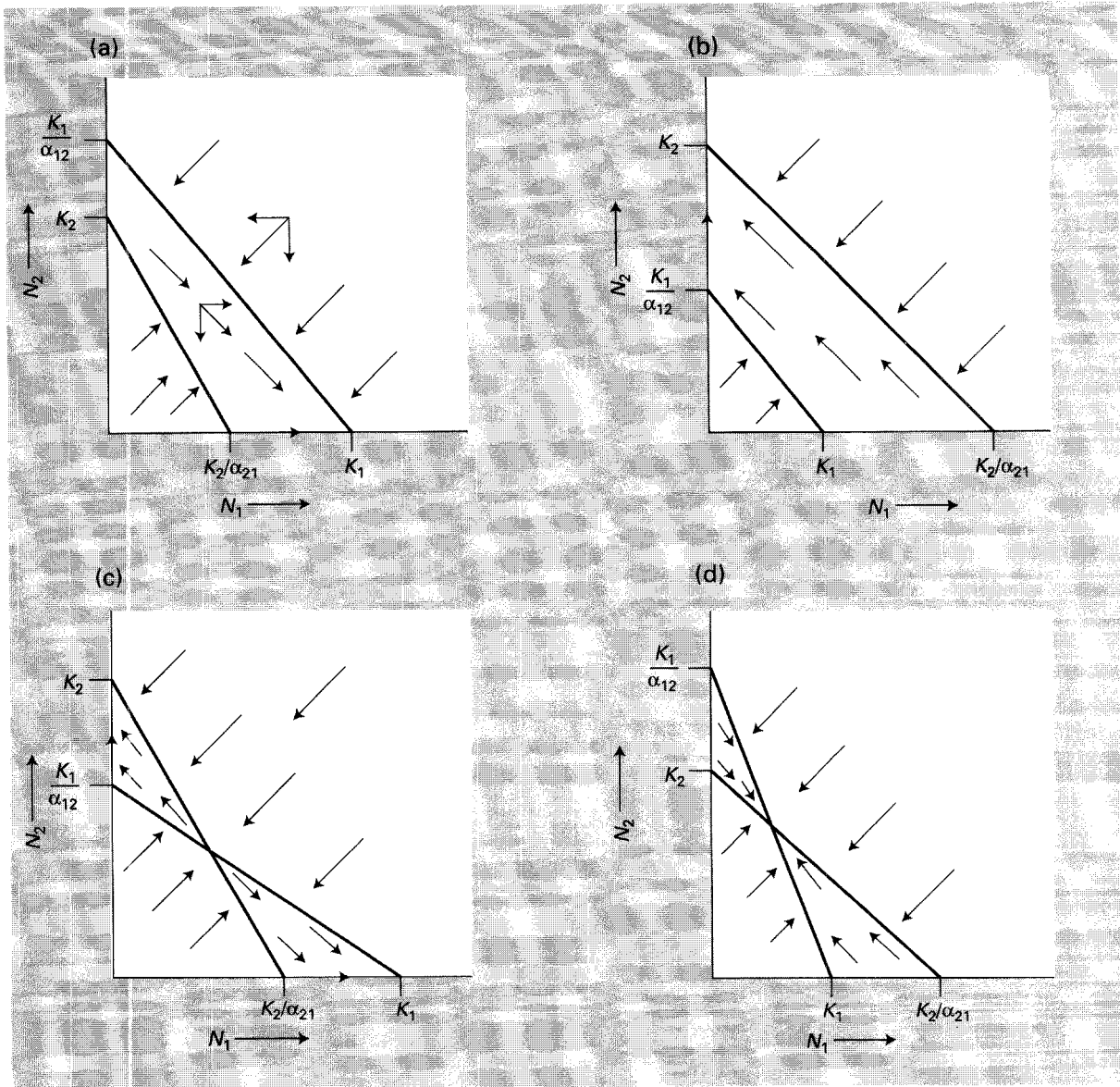


Fig. 4.25 The outcomes of competition generated by the Lotka–Volterra competition equations for the four possible arrangements of the N_1 - and N_2 -isoclines. Vectors, generally, refer to joint populations and are derived as indicated in (a). For further discussion, see text.

important to realize that this model (given ‘experimental teeth’ by the laboratory work of Gause, 1934) was

the original inspiration of the Competitive Exclusion Principle; investigation of the relevance of the principle, and its applicability in the real world, came later. Yet, the most important aspect of the model is that it makes exact, *quantitative* predictions about coexistence, based on the numerical values of the K s and α s. Ultimately the model’s utility must be tested in these quantitative terms.

4.13.2 A test of the model: fruit fly competition

There have been several studies in which experimental results have tended to support the model's predictions. It will be more instructive, however, to consider an example in which results and predictions disagree, because this will illustrate a point of general importance: models are of their greatest utility when their predictions are *not* supported by real data, *as long as the reason for the discrepancy can subsequently be discovered*. Confirmation of a model's predictions represents consolidation; refutation with subsequent explanation represents progress.

Ayala *et al.* (1973) reviewed Ayala's own findings on laboratory competition between pairs of *Drosophila* species. Their results are illustrated in Fig. 4.26. Ayala's basic procedure was to maintain either one- or two-species populations in culture bottles using a 'serial transfer' technique—transferring adults to new food at regular intervals—and to monitor the populations for several generations until an approximate equilibrium was reached. This allowed him to estimate the carrying-capacities (K_1 and K_2) in single-species populations, and the numbers for stable coexistence (\bar{N}_1 and \bar{N}_2) in two-species populations. Figure 4.25d shows that our simple model predicts that stable coexistence should only occur at a point above and to the right of the line joining K_1 and K_2 . It is clear from Fig. 4.26, however, that in seven out of eight cases Ayala found coexistence below and to the left of this line. Our simple model is, therefore, unable to account for Ayala's results.

The simplest explanation for such a discrepancy is illustrated in Fig. 4.27. If the isoclines are concave, rather than straight, the values of K_1 , K_2 , \bar{N}_1 and \bar{N}_2 immediately become compatible. In fact, Ayala *et al.* (1973) were able to support this solution, in a particular species-pair, by following a number of populations for a single generation and obtaining an actual series of vectors. These, too, are shown in Fig. 4.27, in which we can see that the curved isoclines are, indeed, satisfactory lines of demarcation between areas of increase and decrease.

Ayala *et al.* took their analysis a stage further by considering a range of possible alternative models

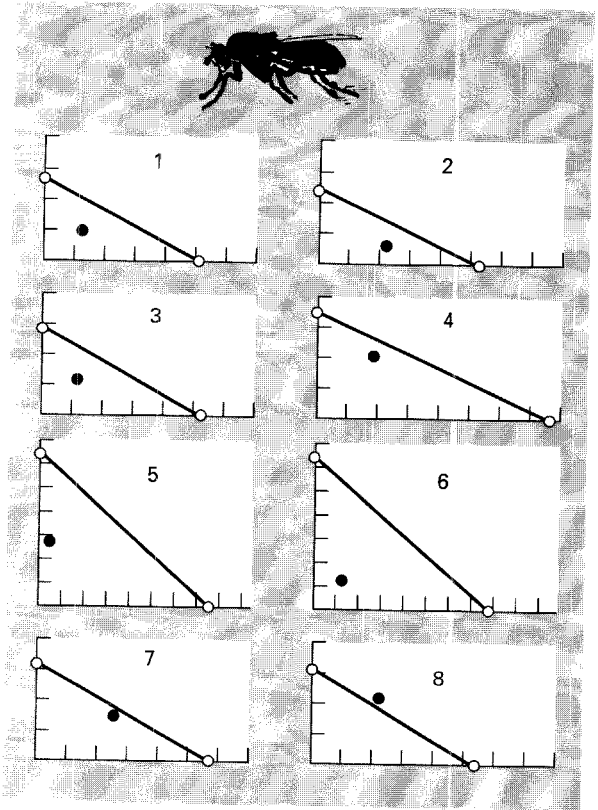


Fig. 4.26 Carrying-capacities (open circles) and stable two-species equilibrium points (closed circles) for eight combinations of two species of *Drosophila*. Each division along the coordinates corresponds to 250 flies. In all but the last case, the point of stable two-species equilibrium falls below the straight line joining the carrying-capacities. (After Ayala *et al.*, 1973.)

which would generate the appropriately curved isoclines. They judged these on a number of criteria, including simplicity, biological relevance of the parameters and quality of fit to the data, and found that one equation was particularly satisfactory. This equation:

$$\frac{dN_i}{dt} = r_i N_i \left(\frac{K_i^0 - N_i^{\theta_i}}{K_i^0} - \frac{\alpha_{ij} N_j}{K_i} \right)$$

is a modification of the original, simple model, but it contains, in addition, a parameter, θ_i , which modifies the underlying logistic equation, such that the function relating growth-rate to density need no longer be

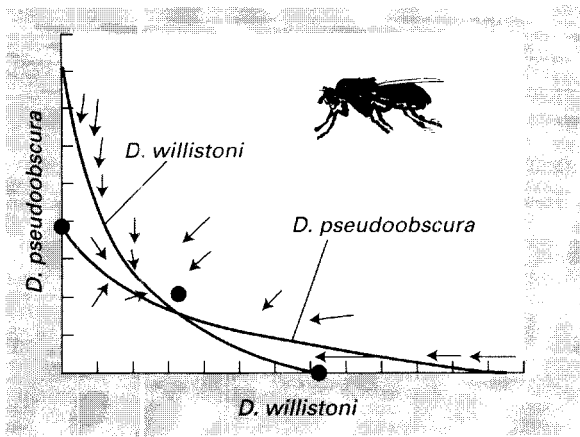


Fig. 4.27 Isoclines for two species of *Drosophila* fitted by visual inspection of the vectors, which were derived empirically and are reduced to one-third of their actual length for clarity. Each division along the coordinates corresponds to 200 flies. Closed circles indicate the carrying capacities and the point of stable two-species equilibrium, which were also derived empirically. (After Ayala *et al.*, 1973.)

a straight line symmetrical about $K/2$. Thus, the work of Ayala *et al.* confirms our original misgivings regarding the incorporation of the logistic equation into our model. It also points to an alternative model which, in quantitative terms, is certain to be more generally applicable than the original. Note, however, that the more qualitative conclusions concerning exclusion and coexistence remain unaffected.

4.14 Analysis of competition in plants

Where competitive outcomes are assessed by additive designs (see Fig. 4.7) the analysis of competition is achieved by the use of yield-density models. These come in a variety of forms depending on the design used and the ability of the model to fit the observed data empirically (Cousens, 1985).

To analyse additive designs we must reconsider the model developed earlier for intraspecific competition (equations 3.5 and 3.6). Hassell and Comins (1976) and Watkinson (1980) have pointed out that this model may be easily extended to include the influence of a second species.

Thus, with a notation similar to that used in equation 3.5 in section 3.2.2 the mean yield \bar{w}_1 of a plant of species 1 in a mixed population containing species 1 and 2, at densities N_1 and N_2 is

$$\bar{w}_1 = w_{m,1} [1 + a_1(N_1 + \gamma_{1,2}N_2)]^{-b} \quad (4.1)$$

in which $\gamma_{1,2}$ is a 'competition coefficient' or 'equivalence value' converting the density of species 2 into numerical terms equivalent to species 1. Likewise, the effect of species 2 on the mortality of 1 is

$$N_1 = N_{i,1} [1 + m_1(N_{i,1} + \delta_{1,2}N_{i,2})]^{-1}$$

where $\delta_{1,2}$ is the appropriate equivalence value determining the density-dependent mortality in species 1 attributable to species 2. This pair of equations can also be written for species 2 with (of course) different equivalence coefficients.

We can appreciate the value of this model by re-examining the data of Marshall and Jain (1969) on oats (see Fig. 4.10). Whereas from our earlier interpretation we could qualitatively conclude that *Avena fatua* was the superior competitor in mixture with *A. barbata* we can now quantify this. Fitting equation 4.1 to the results (Firbank & Watkinson, 1985) gave the following pair of equations:

$$S_B = 188 [1 + 0.41(N_B + 1.44N_F)]^{-0.96}$$

and

$$S_F = 141 [1 + 1.02(N_F + 0.19N_B)]^{-0.72}$$

The subscripts B and F refer to *A. barbata* and *A. fatua*, respectively, whilst S is the mean number of seeds produced per plant and N is the density of each species in the mixture. This pair of equations neatly encapsulates the absolute differences between the two species and their competitive interactions. On average an isolated plant of *A. fatua* produced 47 seeds (188–141) less than *A. barbata* but required more space to do so since its ecological neighbour area (1.02) is larger than for *A. barbata* (0.41). This numerical superiority in seed output is offset, however, by the fact that on a one-to-one basis *A. fatua* is much more competitive as judged by the competition coefficients. In mixture, *A. barbata* 'perceives' each *A. fatua* as equivalent to 1.44 of its own individuals. Each *A. fatua* plant on the other

hand 'perceives' each *A. barbata* plant as about a fifth (0.19) of one of its own. (Note that this analysis does not assume a reciprocity in competition coefficients as in the case of the replacement series.) We can immediately see then that this approach extends our qualitative conclusions about the nature of interspecific interactions.

The 'competition coefficient' in equation 4.1 is density-independent—a 'fixed' value applying to all densities of the second species. In analysing the response surface shown in Fig. 4.11, Law and Watkinson (1987) showed, by careful statistical analysis, that a better fit to the observed data was achieved by a model that allowed competition coefficients to vary both with frequency and density.

The form of model used was

$$\bar{y}_i = y_{mi} / (1 + (N_1)^{b_1} + (N_2)^{b_2}) \quad (4.2)$$

where, following previous conventions, \bar{y}_i is the mean seed yield per plant of species *i*, and y_{mi} is the maximum yield of an isolated plant of species *i*, and N_1 and N_2 are the initial densities of each species. The power terms b_1 and b_2 enable competitive abilities to be described in a density-dependent manner, but it is not possible to attach biological meaning to them in the same way as b in equation 4.1. The estimated parameter values are indicated in the equations 4.3 and the outcome of competition can be determined by iterating them from any initial pair of population densities, $N_{p,t}$ (*Phleum*) and $N_{v,t}$ (*Vulpia*). Note that this model assumes discrete generations of population growth and the seed yield of each species after the action of competition is reduced by 50% to mimic seed losses during the dormant stage of the life cycle.

$$\begin{aligned} N_{p,t+1} &= 0.5 (1160 N_{p,t} / (1 + (N_p)^{1.03} + (N_v)^{1.29})) \\ N_{v,t+1} &= 0.5 (187 N_{v,t} / (1 + (N_v)^{0.637} + (N_p)^{0.834})). \end{aligned} \quad (4.3)$$

Figure 4.28 gives in a joint abundance diagram of the two species the density combinations that give zero population growth for each species—the zero growth isoclines—and some illustrative population trajectories. All of the population trajectories move (usually in a single generation) to the space between the isoclines and then consistently towards the bound-

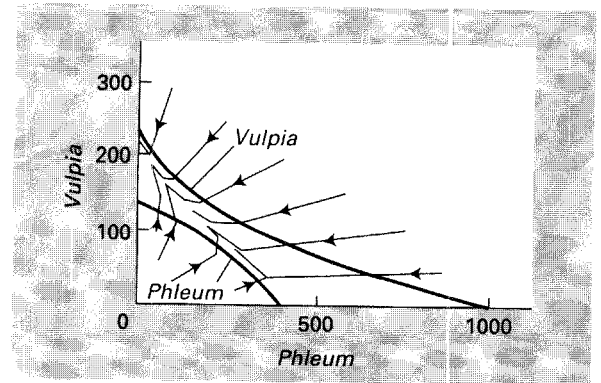


Fig. 4.28 An abundance diagram for *Phleum arenarium* and *Vulpia fasciculata* showing the isoclines (derived from the data shown in Fig. 4.11) and the trajectories (arrowed) illustrating the long-term outcome of competition over succeeding generations. (After Law & Watkinson, 1987.)

ary equilibrium density for *Vulpia* of 227 seeds, with the eventual eradication of *Phleum*. Note that this happens despite the fact that isolated plants of *Phleum* are much more prolific seed producers than *Vulpia*, 1160 as opposed to 187 seeds per plant.

The outcome of competition described by yield-density relationships in the form of equation 4.1 may be analysed in a similar manner on joint abundance diagrams but in actual fact there is an alternative and easier method of analysis. Consider the pair of recurrence equations (4.4) for two species X and Y in which competitive effects are described by an 'equivalence coefficient'.

$$\begin{aligned} N_{x,t+1} &= \lambda_x N_{x,t} / [(1 + a_1(N_{x,t} + \alpha N_{y,t}))^{b_1}] \\ N_{y,t+1} &= \lambda_y N_{y,t} / [(1 + a_2(N_{y,t} + \beta N_{x,t}))^{b_2}] \end{aligned} \quad (4.4)$$

Hassell and Comins (1976) have shown that difference equations of this form are analytically tractable. That is to say, that it is possible by the mathematical technique of phase plane analysis to identify four regions in the parameter space of the coefficients α and β in which different outcomes of competition will occur. In two regions the model predicts that one species will be driven to extinction by the other; in another region stable coexistence of both species will result, whilst in the fourth unstable equilibria may result (Fig. 4.29). Thus from knowledge of the entire

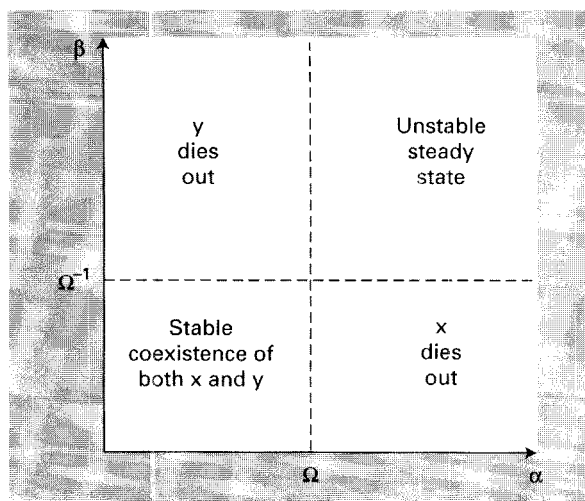


Fig. 4.29 Regions in the $\alpha\beta$ -plane defining the dynamical behaviour of two species interactions governed by equation 4.9. (After Hassell & Comins, 1976.) The boundaries of the four regions are determined by Ω where

$$\Omega = (a_2[(\lambda_x)^{1/b_1} - 1]) / (a_1[(\lambda_y)^{1/b_2} - 1]).$$

See text for details.

set of parameter values, we might make predictions of the long-term outcome. As mentioned above, yield-density responses have long been explored by agronomists seeking models to describe the relationships between crop yield and weed densities in additive competition experiments. Spitters (1983) reviews the range of reciprocal yield models and Mortimer *et al.* (1989) describe their relationship to equations 4.4.

4.15 Niche overlap

We return to the question first posed in section 4.10. How much niche differentiation is necessary for the coexistence of interspecific competitors? We shall see that this question is intimately related to a problem which, in evolutionary terms, confronts all species: that of offsetting interspecific competition against intraspecific competition (section 4.12). There have been several theoretical approaches to the solution of this problem, but since, for the most part, they reach similar conclusions, we can concentrate on the one

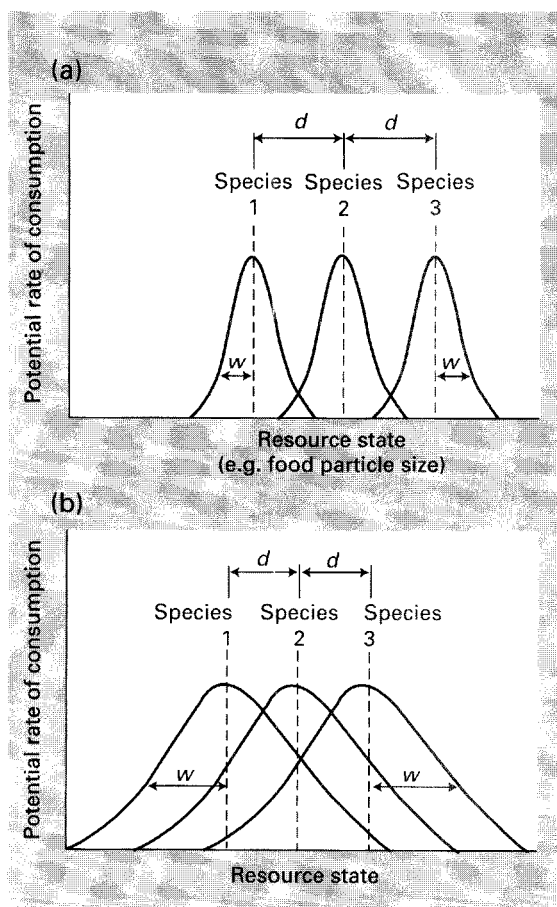


Fig. 4.30 Resource utilization curves for three species coexisting in a one-dimensional niche system; d is the distance between curve maxima, which occur at the centre of the curve; w is the standard deviation of the curves. (a) Narrow niches with little overlap ($d > w$). (b) Broad niches with considerable overlap ($d < w$).

initiated by MacArthur and Levins (1967) and developed by May (1973).

Imagine three species competing for a single, unidimensional resource which is distributed continuously; food size and food at different heights in a forest canopy both conform to this description. Each species has its own niche in this single dimension within which it will (in our examples) consume food. Moreover, its consumption-rate is highest at the centre of its niche and tails off to zero at either end. Its niche

can, therefore, be visualized as a resource utilization curve (Fig. 4.30). Clearly, the more adjacent species' utilization curves overlap, the more they compete. Indeed, if we make the (fairly restrictive) assumptions that the curves are 'normal' (in the statistical sense), and that the different species have similar curves, then the competition coefficient (applicable to both adjacent species) can be related to the standard deviation of the curves, w , and the difference between their peaks, d , by the following formula:

$$\alpha = e^{-\frac{d^2}{4w^2}}.$$

Thus α is very small when there is considerable separation of adjacent curves ($d/w \gg 1$, Fig. 4.30a) and approaches unity as the curves themselves approach one another ($d/w < 1$, Fig. 4.30b).

In terms of this model, we can ask the following question. How much overlap of adjacent utilization curves is compatible with stable coexistence? Obviously, if there is very little overlap, as in Fig. 4.30, there is very little interspecific competition and competitors can coexist. Conversely, in such a case the species have rather narrow niches. This means, since all conspecifics are consuming very similar food, that there is intense intraspecific competition. Moreover, the food items in those positions along the resource spectrum where the curves overlap are being almost totally ignored by the consumers. It is, therefore, likely that natural selection will favour an increased consumption of these neglected food items, an increase in niche breadth, a lessening of intraspecific competition, and thus an increase in niche overlap. The question is: how much?

MacArthur and Levins (1967) and May (1973) answered this question by what was, in essence, an extension of the search for stable coexistence pursued in section 4.1.3. They assumed that the two peripheral species had similar carrying capacities (K_1 , proportional to the area under the utilization curve), and considered the coexistence between them of an intermediate species (carrying capacity K_2). Their results are illustrated in Fig. 4.31, which indicates the values of K_1/K_2 that are compatible with stable coexistence for various values of d/w . At low values of d/w (high α)

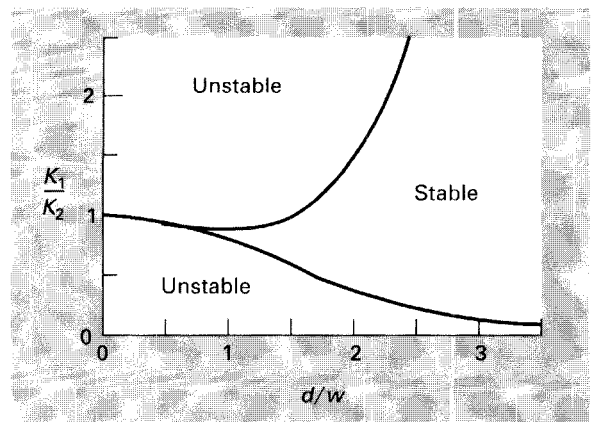


Fig. 4.31 Niche overlap and coexistence. The range of resource utilization (indicated by the carrying capacities, K_1 and K_2 , where $K_1 = K_2$) which permits a three-species equilibrium community with various degrees of niche overlap (d/w). (After May, 1973.)

the conditions for coexistence are extremely restrictive, but these restrictions lift rapidly as d/w approaches and exceeds unity. In other words, stable coexistence is *possible* under the restrictive conditions imposed by low values of d/w , but as May (1973) points out, because conditions are so restrictive '... it may be plausibly argued that environmental vagaries in the real world will upset such an equilibrium'.

So we have seen that high values of d/w there is intense intraspecific competition and underexploitation of resources, and at low values of d/w the equilibrium is too fragile to be maintained in the real world. Theory, therefore, suggests that the coexistence of competitors (using a unidimensional resource) will be based on niche differentiation in which d/w is approximately equal to, or slightly greater than unity. Unfortunately, the testing of this suggestion is hindered by two major problems. The first is that it applies only to situations in which there is a simple, unidimensional resource (probably quite rare), and in which the utilization curves are at least approximately the same as in the model. Competition in several dimensions, and certain alternative utilization curves (Abrams, 1976) would both lead to lower values of d/w being compatible with robust, stable coexistence. The second problem is the collection of the appropriate

data. These are needed in order to establish the dimensionality of competition, and the form of the utilization curve; and also to determine not only d but w as well. Thus, the field evidence persuasively used by May (1973) in support of this model's suggestions was even more persuasively criticized by Abrams (1976). In particular, there is a grave danger, when attempting to 'test' the predictions of this model, that those field examples that support it will be selected, while those that do not support it are ignored. From our own examples, for instance, we could select the ant *Veromessor pergandei* (see Fig. 4.6) and the two hydrobiid snails (see Fig. 4.19) as providing empirical support for the model's prediction ($d/w = 1$). Yet, while such support is gratifying, it most certainly does not prove that the model is correct. What is needed is evidence that such 'supportive' patterns occur much more frequently than would be expected by chance alone; and as yet we have insufficient data to provide this evidence.

Nevertheless, the model has shown us that there is likely to be *some* limit to the similarity of competing species; and that this limit represents a balance between, on the one hand, the evolutionary avoidance of intraspecific competition and the underexploitation of resources, and on the other hand, the evolutionary avoidance of equilibria which are too fragile to withstand the vagaries of the real world. Once again, therefore, a model, without being 'correct', has been immensely instructive.

4.16 Competition and heterogeneity

Most of this chapter has been concerned with competitive situations in which the habitat has remained more or less constant and environmental conditions have remained more or less stable. Under these circumstances the models we have explored, based on intrinsic rates of increase, carrying capacities and competitive abilities, can be expected to give a reasonable description of interspecific competition. Individuals have had time to distribute themselves relatively evenly in the suitable habitats and, as assumed by the classical theory, each individual encounters about the same number of conspecific and heterospecific com-

petitors. However, for many competing species, habitats are often less predictable and shorter lived. Many species exploit resources which are divided into small, discrete patches, such as carrion, dung, fungi or fruit. In these patches there is often time for just one generation before the resource unit (patch) becomes unusable. Here, species' competitive abilities are not the only determinants of coexistence or competitive exclusion.

Atkinson and Shorrocks (1981) explored by computer simulation, and Hanski (1981) by a simple analytical model, ways of incorporating habitat heterogeneity into competition models. They examined the effect of resource subdivision on two species competition and found that their coexistence could be facilitated by dividing the resource into more and smaller breeding patches, assuming that the distribution of individuals was aggregated over those patches. The opposite of an aggregated distribution is an even distribution when each patch contains an equal number of competitors. If both competitors were evenly distributed then the inferior competitor would come into conflict with the superior competitor on every patch and would be eliminated. This is not the case with aggregated distributions, when, depending on the level of aggregation, many individuals of the inferior competitor meet few, if any, individuals of the superior competitor. In particular, the models of Atkinson and Shorrocks and of Hanski demonstrate the possibility of continued coexistence of an inferior with a superior competitor, when the two species have independently aggregated distributions over the resource patches. Coexistence occurs because the competitive pressure of the superior competitor is largely directed—as a result of aggregation—at members of its own species, those present in the high density patches. In other patches, the superior competitor will be scarce or absent, and here the inferior competitor is able to escape interspecific competition. In other words, coexistence is facilitated because the variation in population densities among the habitat patches shifts the balance from interspecific towards more intraspecific competition. It should be noted that if two species do not have relatively independent distributions but have a tendency to aggregate in the same

patches, then coexistence is less likely. Thus habitat patchiness itself is not critical; the important question is how that heterogeneity is perceived by individuals.

Rosewell *et al.* (1990) and Shorrocks *et al.* (1990) have tested the assumptions of the aggregation model of coexistence using 360 data sets, largely for drosophilid flies—the group that inspired the original model. The assumptions tested were that: (i) the competing individuals (larvae) are aggregated; (ii) the degree of aggregation can be represented by a parameter (k of the negative binomial distribution) which remains the same at different overall densities; and (iii) there is no strong association between species. The vast majority (93%) of the data sets showed larval aggregation, so the first assumption was upheld: competing stages are strongly aggregated. Of the data sets 79% were adequately described by a negative binomial distribution. The assumption that aggregation (as measured by the parameter k of the negative binomial distribution) does not change with density was less well supported. Aggregation declined at higher densities and thus coexistence may be less likely in larger patches (see also Shorrocks & Rosewell, 1987). Even if this second assumption is relaxed, however, the predictions of the model remain essentially unchanged. The final assumption, that species utilizing patchy resources are distributed independently of each other was potentially a complicating factor for the two-species model, but in only 5% of possible comparisons examined were significant associations found. Thus coexistence of two species with independently aggregated distributions is likely in situations in which one or other of the species would have been eliminated in a homogeneous environment.

Studies on the coexistence of competitors on ephemeral resources have not been restricted to fruit flies. Hanski and Kuusela (1977), Hanski (1987) and Ives (1991) have looked at aggregation and coexistence in carrion fly communities (the community of flies whose larvae feed on dead animals, usually vertebrates). In Hanski and Kuusela's study, 50 small pieces of carrion were laid out in a small area and natural colonization was permitted to take place. A total of nine species of carrion fly was recovered from the patches, but the mean number of species emerging

per patch was only 2.7. All nine species showed highly aggregated distributions and particular pairs of species came into contact only rarely, thus interspecific competition was much less intense than might have been expected on the basis of the number of species and number of patches present. Ives (1991), by a mixture of experiment similar to that described above, and theory, has estimated that the effect of aggregation on coexistence for the five carrion fly species present in his study was equivalent to reducing the amount of larval competition between pairs of species by an average of at least 57%.

The aggregation model predicts that coexistence of many species is often dependent on their independently aggregated spatial distributions. Hanski (1987) has tested this prediction with a field experiment with blowflies. Female flies were allowed to oviposit for 3 days on small carcasses placed at 15 m intervals in a homogeneous field. After the oviposition period, the

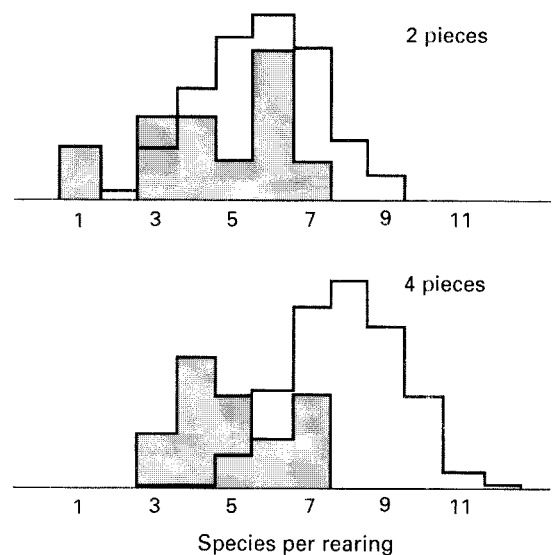


Fig. 4.32 Comparison between the control and experimental rearings in species number. The open histogram is the null hypothesis, derived by pooling flies from each combination of two and four of the 20 control rearings ($n = 190$ and 4845, respectively). The number of experimental rearings was 11 (two pieces) and nine (four pieces). Removing resource patchiness increases the dominance of the best competitor and decreases species richness. (From Hanski, 1987.)

carcasses were removed from the field and placed in containers to rear the flies out. In the control rearings, each carcass was placed in its own container, whereas in the experimental rearings two or four carcasses were placed next to each other in the same container. In the experimental rearings fly maggots could easily move from one carcass to another, and thereby density variation among the carcasses placed in the same container was effectively removed. Figure 4.32 shows that decreasing larval aggregation (the experimental rearings) decreased the number of fly species emerging from the rearing, in comparison with the expected results calculated from the control rearings. This result directly demonstrates how the aggregated spatial distribution of fly maggots among replicate

carcasses maintains species richness in this community.

There seems little doubt that aggregation plays a major role in explaining the coexistence of competitors on divided and ephemeral resources that would exclude one another on resources that were more homogeneous in space and time. Although insects living in carrion, dung, fruit or fungi may be extreme examples of species exploiting patchy habitats, they should not be regarded as exceptions to a rule of habitat homogeneity, rather as one end of a continuum. All habitats are patchy and ephemeral to a degree, hence the theory outlined in this section can be expected to be applicable to many communities of competitors.